RELATIONSHIP BETWEEN SEED DORMANCY AND PERSISTENCE OF SEEDS OF ANNUAL RUDERAL SPECIES IN THE SOIL SEEDBANK

BY

XIANHUI FU

DISSERTATION

Submitted in partial fulfillment of the requirements
for the degree of Doctor of Philosophy in Natural Resources and Environmental Sciences
in the Graduate College of the
University of Illinois at Urbana-Champaign, 2013

Urbana, Illinois

Doctoral Committee:

Associate Professor Adam S. Davis
Professor Jeffrey D. Brawn
Associate Professor Angela D. Kent
Associate Professor James Dalling

ABSTRACT

Knowledge related to seed persistence in soil is critical for weed control decisions in the integrated weed management systems. Many annual weed species have dormant soil seed banks (SSBs), and this may be an important mechanism for seed persistence in these species. Although the relationship between seed dormancy and persistence in soil has received previous attention, it has not been well characterized. In order to quantify the relationship between seed persistence and dormancy, a five-year seedbank dynamics field study was conducted in Savoy, IL, involving twelve ruderal weed species: *Abutilon theophrasti*, *Alliaria petiolata*, *Amata tuberculatus*, *Ambrosia trifida*, *Chenopodium album*, *Ipomoea hederacea*, *Kochia scoparia*, *Panicum miliaceae*, *Polygonum pensylvanicum*, *Setaria faberi*, *Setaria lutescens*, and *Thlaspi arvense*. Seed half-lives ($t_{0.5}$) in the SSB ranged from 0.25 to 2.22 years for the study species. Seed dormancy showed a positive linear relationship to $t_{0.5}$ (slope = 0.050, $p < 0.001$, $R^2 = 0.92$), while the variance of seed dormancy followed a negative nonlinear relationship with $t_{0.5}$. No relationship between environmental conditions during the course of seed burial and seed dormancy across study years was detected. These results indicate a strong relationship between the dormancy and persistence of seeds of ruderal weed species in the soil seedbank. Moreover, they suggest that dormancy release for these species was at least partially controlled by intrinsic seed characteristics. Findings of this study will facilitate the determination of seed persistence and management of the SSB in integrated weed management.

Dedicated to Dengyun and Jing.

ACKNOWLEDGEMENTS

This project would not have been possible without the support of many people. First of all, I want to express great gratitude to my advisor, Dr. Adam S. Davis, for proposing this special project for me and all his advices, encouragements, and supports. It has been a privilege to work with him and learn from him. I am also indebted to my committee members, Dr. Jeffrey D. Brawn and Dr. Angela D. Kent from the Department of Natural Resources and Environmental Sciences (NRES), Dr. James Dalling from the Department of Plant Biology who generously shared their knowledge and advices. I also thank Dr. Joanne Chee-Sanford for her training on molecular technology and microbial ecology. I also thank Dr. Min Cao, who introduced me to the interesting research area of SSB, for his encouragements. In addition, I thank Dr. Xiaoming Zou for his encouragement on pursuing my degree in a totally different environment.

I also want to thank the International Fellowship Program (IFP) of Ford Foundation in China, the Institute of International Education (IIE) that initiated this journey to pursue my Ph. D., a life-changing process, by financially funding me for a three-year fellowship program. I also thank all officials, especially Mr. Keith Clemenger, Ms. Lili Jiang, Ms. Dongsong Yang, Ms. Zhuoga Wang, Ms.Tommy Langan, and Mr. John Brady from both IIE Beijing and IIE New York, and many 2003 IFP alumni who encouraged, supported, and helped me to survive all the difficulties on the way to my degree. I thank the leadership group, faculties, and staffs from my mother unit, Xishuangbanna Tropical Botanical Garden of the Chinese Academy of Sciences in China (XTBG) for their generous supports and encouragements. I thank Dr. Shujin Hu from North Carolina State University

(NCSU), Dr. Liqing Sha from XTBG, and Dr. Rensen Zeng from South China Agricultural University (SCAU) for their encouragements and help.

The faculty, staff, and graduate students in NRES, Agricultural Research Service at United States Department of Agriculture (ARS-USDA), Department of Crop Sciences (CPSC), and the Program in Ecology, Evolution, and Conservation Biology (PEEC) provided a friendly and motivated environment in which to study and work. I want express the particular gratitude to Dr. Jeffrey D. Brawn, Dr. Angela D. Kent, Ms. Piper A. Hodson, and Ms. Karen M. Claus. They make the department like a home to me and I can always find all the help I need. I thank the faculties and staffs at Graduate School and International Student and Scholar Services Center (ISSS) for their help and wonderful services. I thank ARS-USDA for allowing me the use of all the field and molecular lab facilities, equipment and supplies. I thank the staffs at Northern Illinois Agronomy Research Center of University of Illinois Extension at DeKalb, especially Mr. Lyle Paul for providing facilities, logistical support, and permission to conduct this research at this center, for his wonderful maintenance and historical material on my research plots. I thank Dr. Martin M. Williams II, Dr. Darin M. Eastburn, and Dr. John B. Masiunas for all their help. I also thank Mr. John Frihauf and Mr. James Moody for their generous help with the setting up of my field experiments and samplings, and Ms. Lynn Connor and Ms. Terry Holman for their lab training, advices, unselfish help and friendship throughout my stay. I thank all the undergraduate students who ever worked in our lab and helped me with my research. I also thank Dr. Brian Schutte, Dr. Natalie West, Dr. Allana Welsh, Yi Lou, Ramdas Kanissery, Meng Li, and Dr. Eunsoo Choe for discussing my project with me and sharing their suggestions on data analysis. I thank Dr. Angela Kent and Dr. Tony

Yannarell and their graduate students for their kindness and generosity to include me in their group meeting and share their research experience.

Many friends have provided laughter, encouragement, and all types of help and support along the journey. I want to take advantage of this opportunity to express my gratitude to all of them.

During the time of my study, my beloved husband Dengyun and Son Jing provided their unselfish love and support. Meanwhile, they sacrificed a lot of their life for me. My parents also gave me their great love, support, and encouragement. Finally, none of this would have been possible without the unwavering love and support of my siblings, who took care of my parents while I was pursuing my studies.

TABLES OF CONTENTS

LIST OF ABBREVIATIONS

ABA	Abscisic acid
AMS	Accelerator mass spectrometry
ARS-USDA	Agricultural Research Service at United States Department of Agriculture
C	Competition strategy
CPSC	Department of Crop Sciences at University of Illinois at Urbana-Champaign
IFP	International Fellowship Program
IIE	Institute of International Education
ISSS	International Student and Scholar Services Center at University of Illinois at Urbana-Champaign
MD	Morphological dormancy
MPD	Morphophysiological dormancy
NCDC	National Climate Data Center
NCSU	North Carolina State University
Nlm	Nonlinear model
NRES	Department of Natural Resources and Environmental Sciences at University of Illinois at Urbana-Champaign
PD	Physiological dormancy
PEEC	The Program in Ecology, Evolution, and Conservation Biology at University of Illinois at Urbana-Champaign
PY	Physical dormancy
PY + PD	Combination dormancy
R	Ruderal strategy
RCBD	Randomized complete block design
S	Stress strategy

SCAU	South China Agricultural University
SMP	Soil matric potential
SSB	Soil seedbank
STM^2	Soil Temperature and Moisture Model
$t_{0.5}$	Half-life of a seed
TZ test	Tetrazolium test
XTBG	Xishuangbanna Tropical Botanical Garden of the Chinese Academy of Sciences

CHAPTER 1: INTRODUCTION

LITERATURE REVIEW

1.1 SOIL SEEDBANKS (SSBs)

As an important demographic stage, seeds play a critical role in the life cycle of plants. Naturally buried seed reserves, soil seedbanks (SSBs), are comprised of viable seeds that can geminate or have potential to germinate in the future (Harper 1977, Radosevich et al. 1997, Csontos 2007). SSBs play important roles in plant population establishment, survival, recruitment, and regeneration (Dalling et al. 1998a, Dalling et al. 1998b, Cao et al. 2000, Nathan and Muller-Landau 2000, Leck and Schutz 2005, Tang et al. 2006, Li et al. 2010). Maintenance of SSBs can reduce the risk of mortality derived from unfavorable environmental conditions at germination seasons over time and space. Due to the potential for building up a diverse species composition over time, SSBs are considered an important resource for ecological restoration of degraded habitats, such as abandoned slash-and-burn lands (Cao et al. 2000, Fu 2002, Tang et al. 2006), mining sites (Baig 1992, Grant et al. 1996, Carrick and Kruger 2007), and agricultural lands (Bakker et al. 1996, Bakker and Berendse 1999, Garcia-Orth and Martinez-Ramos 2008, Wade et al. 2008). However, SSBs are also the greatest source of weed infestation in arable fields (Cavers and Benoit 1989, Cavers et al. 1992) and are potential sources of invasive species (Cook et al. 1996, An et al. 2007, Kinter et al. 2007). SSBs are considered critical components of ecological based weed management strategies and invasive species management. A comprehensive understanding of the characteristics, dynamics, and mechanisms of seedbank persistence and depletion is therefore critical for

plant species management in both natural and agricultural ecosystems and restoration ecology.

1.1.1 CHARACTERISTICS OF NATURAL SOIL SEEDBANKS (SSBs)

Species composition, seed population density, and seed persistence are important characteristics of a natural soil seedbank. Typically, SSB studies have focused on estimating seedbank density and composition, the two most important characteristics to describe a soil seedbank. Seedbank population densities range from hundreds to more than 150,000 seeds m^{-2} of annual weed species in arable land (Forcella et al. 1992, Radosevich et al. 1997). In contrast, seed population densities in natural forest communities are reported to be lower; for example, in Asian-Oceanic sites seed population densities ranged from 60 to 5,415 seeds m^{-2} (Liew 1973, Cao et al. 2000, Tang et al. 2006), and seed population densities in European temperate forest ranged from 85 seeds m^{-2} (deciduous forest) to 46,224 seeds m^{-2} (succession on heath land in Scotland, UK) (Donelan and Thompson 1980, Hester et al. 1991, Bossuyt and Hermy 2001). The seed population density in a fragmented secondary forest in South West China was estimated at 72,571 seeds m^{-2}, and was comprised of nearly 50% weed species (Cao et al. 2000).

The key procedures for the estimation of SSB population density are separating seeds from soil and determining the viability of the recovered seeds. Greater efforts have been put into developing methods for studying SSB density since Darwin first estimated the number of seeds using samples collected from the bottom of a lake by seedling

emergence (Darwin 1859, Fenner 1991). Generally, the methods can be categorized into two groups: seedling emergence and physical separation of seed from soil.

The method of seedling emergence involves the spreading of a soil sample in a greenhouse space as a shallow layer for a period of time to make sure as many as possible viable seeds emerge from soil. Seedling emergence is the most commonly used method (Roberts 1981) that simultaneously provide information of the count of seed and viability. It can also be easily conducted in most circumstances. However, it usually underestimates seed density because of following reasons:

First, the method of seedling emergence usually counts emerging seedlings, but some seeds experience fatal germination, and die before they emerge from the soil. Second, the environmental conditions as set cannot meet the requirements for all species in the SSB, resulting in seeds of some species not being able to emerge during the time span of the emergence experiment (Roberts 1981, Gross 1990). Third, there are many seeds in the SSB that remain dormant or do not germinate during the course the experiment. Finally, it requires considerable space for the large number of samples and for some research may need longer time (Brown 1992, Bernhardt et al. 2008).

The method of physical separation of seed from soil includes hand-sorting (Price et al. 2010), sieving (wet or dry) (Leon 1980, Cardina and Sparrow 1996), flotation with different salt solutions (Malone 1967, Brown 1992, Buhler and Maxwell 1993, Tsuyuzaki and Kanda 1996, Tsuyuzaki and Goto 2001), or elutriation (Gross and Renner 1989, Gross 1990, Wiles et al. 1996).

Among the physical separation approaches, hand-sorting is useful to protect the integrity of seed. If hand-sorting is performed carefully, specimens can be subjected to

minimal disturbance, which is critical for doing some downstream research such as research on the microbial communities associated with seed. Hand-sorting is appropriate for seed of certain size, but is more challenging for smaller seeds that are found in soil seedbanks. Sieving, floatation, and elutriation may dramatically reduce the labor requirement for separating seed from soil. There are two types of sieving: dry and wet. Air-dried soil samples are often used for dry sieving, whereas wet sieving uses water to wash seed out from soil. Floatation with different salt solutions can effectively separate seed from soil. However, some salt solutions may influence the viability of seeds and are only good for certain species. It is also not good for organic soil samples. Elutriation, actually an advanced format of wet sieving using an automatic soil washing device, is useful for dealing with a large amount of soil samples in a short time period that is required to avoid the inherit issues of spatial heterogeneity of SSB research. However, it is also problematic for differentiating species with small seeds.

When using the method of the physical separation of seed from soil, a viability test is needed because through the method of physical separation both viable and non-viable seeds are extracted. In addition to the two commonly-used viability test methods, tetrazolium test (TZ test) and seedling emergence, the imbibed crush test is an easy and time saving approach for determining seed viability which can be an potential alternative of TZ test in large scale studies of SSBs (Borza et al. 2007). Physical separation, combined with a suitable approach for viability testing, may provide more accurate information of the seedbank density. None of the methods is perfect. Combination of multiple methods is suggested according to the objectives of a project.

Seed persistence, the capability for seed of a species to remain viable and non-geminated in soil for a period of time via various mechanisms (Thompson 2000, Walck et al. 2005), is an important characteristic of SSB of different species. Seed persistence is usually used as a standard to classify soil seedbanks (Thompson and Grime 1979, Grime 1981, Villiers et al. 2002, Csontos and Tamas 2003, Walck et al. 2005). Thompson and Grime (1979) established a functional seedbank classification system in which four categories of seedbanks were identified: transient seedbanks (type I and type II) where seeds last less than one year and persistent seedbanks (type III and type IV), where seeds last longer than one year. Modification of this SSB classification system was made by combining the characteristics of seed germination, dormancy, light requirement for germination, and seed longevity, thus divided type I seedbank into four subcategories, and type III into another two subcategories (Grime 1981). Later on, a five-year-threshold was applied to separate short-term persistent and long-term persistence seedbank that declares if a SSB can persist in soil over five years, then the SSB is long-term persistent, otherwise it is short-term persistence (Bakker et al. 1991, Thompson 1993, Bakker et al. 1996, Thompson et al. 1997, Walck et al. 2005).

Seedbank longevity of a species is difficult to determine under natural circumstances. To collect seed longevity data, few long-term seed burial studies have been conducted since the first soil seed reservoir that was reported in 1859 by Darwin (Darwin 1859, Darlington 1922). A long-term seed viability experiment initiated by Dr. William James Beal indicated that the seed longevity of *Verbascum blattaria*, *Verbascum* sp. and *Malva rotundifolia* could last up to 120 years (Telewski and Zeevaart 2002). Research on seeds recovered from a historical site reported that seeds of *Medicago*

polymorpha, *Malva parviflora*, and H*ordeum leporinum* could persist as viable seed up to two hundred years (Spira and Wagner 1983). Longevity of seed of *Chenopodium album* could last even longer than 1,500 years according to archaeological date (Odum 1965). Long-term seed burial studies are often time-consuming, expensive, and difficult to maintain.

Accelerator mass spectrometry (AMS) technology was used to carbon-date naturally dispersed seeds of three tree species persistent in the top soil layer in Neotropical forest (Dalling and Brown 2009). The study found that tree species *Zanthoxylum*, *Tremam*, and *Croton* could remain viable in the surface layer of SSBs in Neotropical forest after 18, 31, and 38 years burial (Dalling and Brown 2009). AMS technology is a quick method for seedbank persistence determination. However, the high cost of AMS limits the number of repeated measurement in a research and thus, the application of this technology in the SSB studies (Dalling and Brown 2009).

Seed persistence is a species-specific characteristic that is closely related to seed size (Bekker et al. 1998, Thompson et al. 1998, Moles et al. 2000, Peco et al. 2003, Harrison et al. 2007, Pringle et al. 2007, Schutte et al. 2008b), seed shape (Bekker et al. 1998, Thompson et al. 1998, Moles et al. 2000, Peco et al. 2003), seed coat hardness (Pringle et al. 2007) and thickness (Gardarin et al. 2010), seed germination physiology (Grime 1981, Thompson et al. 1998, Moravcova et al. 2006), seed dormancy characteristics (Thompson and Grime 1979, Grime 1981, Leck and Schutz 2005, Van Klinken et al. 2008), and mechanisms of defense of a seed against predators or pathogens (Thompson et al. 1998, Davis et al. 2008, Dalling et al. 2011). Moreover, maternal environment during seed maturation (Fenner 1991, Schutte et al. 2008a), burial depth

(Conn et al. 2006, Davis and Renner 2007, Harrison et al. 2007), and environmental conditions of burial site, e.g., soil temperature (Lonsdale 1993, Benech-Arnold et al. 2000, Leishman et al. 2000, Ooi 2012), moisture (Schafer and Chilcote 1970, Schafer and Kotanen 2003, Mollard and Insausti 2009, Pakeman et al. 2012), light (Pons 2000, Goggin and Steadman 2012), agricultural practices (Froud-Williams et al. 1983, Sternberg et al. 2003, Gallandt et al. 2004), land use history (Bossuyt and Hermy 2001), and other biological factors like dispersal (Bakker et al. 1996, Dalling et al. 1998a, Harrison and Regnier 2003, Davis and Raghu 2010, Dalling et al. 2011), predation (Harrison and Regnier 2003, Davis and Raghu 2010, Dalling et al. 2011), and pathogens (Pitty et al. 1987, Chee-Sanford et al. 2006, Davis and Renner 2007, Wagner and Mitschunas 2008) also influence seed persistence in soil.

1.1.2 SOIL SEEDBANK DYNAMICS AS A COMPONENT OF INTEGRATED WEED MANAGEMENT

Because of their economic importance, SSBs in arable lands have received much attention and have been extensively studied (Cavers and Benoit 1989). Weed species are usually characterized by high fecundity, producing a large number of seeds in various environments (Cavers and Benoit 1989, Booth et al. 2003). Seeds of annual weed species account for the majority of seedbank inputs in various arable habitats (Cavers and Benoit 1989, Cao et al. 2000, Tang et al. 2006). Maximum seed population density in arable land as high as 930,910 seeds m^{-2} has been reported in Malaysia (Sahid 1995, Baskin and Baskin 2006). The large amount of weed seeds stored in SSBs accounts for the future infestation of weed in crop lands and other habitats. Dormant seeds in soil may extend the

duration of seed germination and seedling emergence, leading to temporal escape from weed control measures, thus increasing the challenge of weed management.

Interest in weed control strategies involving weed SSB management has received increasing attention over the past 20 years. SSBs are considered an important component for long-term decision-making because weed seedbank populations in the soil may lead to crop-yield reductions in future seasons (Sahid 1995, Hughes and Andujar 1997). The reduction of seed persistence of problematic weed species has remained a critical goal for long-term crop management in agriculture (Davis 2006). Germination, seed aging, seed predation (Fenner and Thompson 2005, Menalled et al. 2006, Davis and Raghu 2010), and biologically-mediated seed decay are frequently regarded as major causes of seedbank loss. Even though soil amendment with organic residues (Gallandt et al. 1999, De Cauwer et al. 2010), application of nitrogen fertilizer (Davis 2007), soil tillage (Cardina et al. 1991, Mulugeta and Stoltenberg 1997, Ghersa and Martinez-Ghersa 2000, Gallandt et al. 2004, Davis et al. 2005b), cover cropping (Davis 2008, Mirsky et al. 2010), and crop rotation (Mulugeta and Stoltenberg 1997, Cardina et al. 2002, Davis et al. 2006) are practices that affect SSBs, the mechanistic details associated most particularly with seed decay processes have not been well elucidated (Chee-Sanford et al. 2006).

Manipulation of SSBs in soil has been suggested as a central aim of successful weed management in agro-ecosystems (Kremer 1993). Knowledge of mechanisms regulating the fate of weed seeds in soil is critical for the development of long-term and sustainable weed management strategies. Understanding the dynamic processes that drive the fates of seeds in SSBs is one of the greatest challenges of SSB management (Forcella

et al. 1996, Buhler et al. 1997, Dekker 1997). Despite the potential for large benefits to weed management gains through improved SSB management, information about ecological drivers of seed fates, especially patterns of seed loss and the variability of loss under different environmental and agricultural conditions in SSBs is mostly lacking.

1.2 SEED DORMANCY

Seed dormancy is an internal condition of the seed that prevents germination of viable seeds under environmental conditions proper for seed germination (Benech-Arnold et al. 2000, Allen et al. 2007). This process helps to prevent local extinction of a plant species due to seed germination before their dispersal from their parent plants or under environmental conditions unfavorable for seed germination or seedling establishment. It has been regarded as a "bet-hedging" strategy for plant species, especially annual species that have a dormant SSB (Rees 1997, Fenner and Thompson 2005): by spreading the germination of a given cohort of seeds over a number of years, plants may increase their fitness by buffering their offspring against temporal fluctuations in conditions suitable for establishment and reproduction. This is especially important to weeds of arable systems, in which human-mediated disturbances fluctuate somewhat independently of environmental variation, driven primarily by farmer choices about crop sequence and management tactics linked to markets and personal preferences. Seeds with different types of dormancy may undertake various defense mechanisms to protect them from natural enemies such as pathogens or herbivores they may encounter in the natural habitats and thus, influence the dynamics and distribution of plant species across ecosystems (Dalling et al. 2011). Understanding of seed dormancy classification systems

may be helpful for determining how seeds defend themselves and developing effective weed management strategies.

1.2.1 CLASSIFICATION OF SEED DORMANCY

There are multiple seed dormancy classification systems available. At the most basic level, seed dormancy is categorized as either primary or secondary dormancy according to the time seed dormancy develops in relation to the time of seed dispersal from the mother plant (Karssen 1982). Primary dormancy refers to the innate dormancy possessed by seeds at the time they are dispersed from the mother plant. Secondary dormancy refers to seed dormancy induced after seed dispersal, brought on by environmental conditions unfavorable for germination (Foley 2001, Allen et al. 2007). The first comprehensive dormancy classification system was developed by a Russian seed physiologist Marianna G. Nikolaeva (Baskin and Baskin 1998, Baskin and Baskin 2004). A modified version of Nikolaeva's seed dormancy classification scheme was suggested by Baskin and Baskin (2004). The modified seed dormancy classification system includes five classes of dormancy: physiological dormancy (PD), morphological dormancy (MD), morphophysiological dormancy (MPD), physical dormancy (PY), and combination dormancy (PY + PD) (Baskin and Baskin 2004). Among the five classes of dormancy, PD, MD, and PY are three fundamental dormancy types (Baskin and Baskin 1998, Fenner and Thompson 2005). Seeds with PD are dormant due to physiological inhibiting mechanisms of seed germination in the embryo. For example, presenting of plant growth regulator abscisic acid (ABA) would result in PD (Baskin and Baskin 2004). Embryos of seeds with PD are usually full developed and dormant (Baskin and Baskin 1998, Baskin and Baskin 2004). Seeds with MD are usually immature at the time when

they are shed and after-ripening is required for germination to occur. Seed embryos with MD are underdeveloped but non-dormant, becoming germinable once they have reached maturity (Baskin and Baskin 1998, Baskin and Baskin 2004). Seed coats (or pericarps) impermeable to water form the basis for physical dormancy. Embryos of seeds with PY are fully developed and can germinate once protecting integuments become permeable to water (Baskin and Baskin 1998, Baskin and Baskin 2004). In quiescence state [enforced dormancy according to Harper (1977)], a seed cannot germinate because of the absence of one or more of required environmental factors but it can germinate when environmental conditions are within its range of requirements for radicle emergence. Therefore quiescence is distinct from dormancy as a mechanism for preventing the germination of viable seeds (Baskin and Baskin 2004). Differentiation quiescent seed from dormant seeds is particularly important for research to quantify the relationship between seed dormancy and other seed features.

1.2.2 SEED DORMANCY AND SEED PERSISTENCE IN SOIL

The relationship between seed dormancy and seed persistence has is the subject of an ongoing debate in the scientific literature. One side of the argument assumes that seed dormancy is a critical mechanism for persistence in SSBs, a view taken particularly by those focusing on seedbank dynamics of weeds in arable systems (Booth et al. 2003). The definitions of SSB provide evidence for this argument (Harper 1977, Roberts 1981, Csontos 2007). For example, SSBs refer to all viable seeds (dormant with potential to germinate) on the soil surface or in soil (Roberts 1981, Simpson et al. 1989). Others have made strong claims seed dormancy and persistence are not necessarily associated with (Thompson et al. 2003) or not an essential part of seedbank formation (Honda 2008).

However, the relationship between seed dormancy and seed persistence in SSB has not yet been well examined with empirical studies.

Plant species have developed various strategies to increase the possibility of seed survival under unfavorable environmental conditions and thus, influence seed persistence in soil. Certain types of seed dormancy may therefore be restrained to specific habitats or ecosystem types (Dalling et al. 2011). A species with PD seed may rely on both physical and chemical mechanisms to defend against threats to the seed. The contribution of each mechanism depends on the pressure of soil pathogen and duration of seed persistence (Dalling et al. 2011). PD may dominate in dry or well-drained habitats with relatively low pathogen pressure. In contrast, seeds of species with PY depend on their physical structure such as impermeable seed coats or pericarps to protect them from the attack of predators and pathogens (Baskin and Baskin 1998, Davis et al. 2008, Dalling et al. 2011). PY might be favored in warm and moist habitats of high pathogen pressure such as tropical forests. Species with transient SSBs depend more on chemical defense, while species with highly persistent SSB relatively more depend upon physical defense (Davis et al. 2008). Improved knowledge of mechanisms of seed dormancy related to seed persistence in soil will influence the strategies on management of weed SSBs in relation to the integrated weed management.

1.3 RUDERAL SPECIES

Grime (1974, 1977) proposed a conceptual model to describe the responses of the vascular plants to the stress and disturbance from different habitats. In his system, stress refers to all possible external limitations on rate of dry-matter production, whereas

disturbance refers to mechanisms that reduce plant biomass through partial or total destruction such as natural disaster events or tillage in arable land. Three extreme plant strategies including competition (C), stress (S), and ruderal (R), were posited to exist at the vertices of a triangle representing plant adaptive strategies to stress and disturbance in their habitats (Grime 1977, Booth et al. 2003). Combinations of low stress and low disturbance, high stress and low disturbance, and low stress and high disturbance are associated with the evolution of C strategy, S strategies, and R strategies respectively (Grime 1974, 1977). Most annual weed species follow an R strategy, which is analogous to r-selection (Grime 1977, Booth et al. 2003).

Ruderal species colonize habitats that have been disturbed, such as road sides or waste ground. Some common features evolved for ruderals to adapt to persistent and severe disturbance include short life cycles (annual or short-lived perennial), rapid growth, and large investment to reproduction (seeds) (Grime 1974, 1977, Booth et al. 2003). These features of ruderals make them pre-adapted to colonize highly disturbed but productive arable land as weeds of agriculture. The short life span and large number of seeds produced by ruderal species allow them to re-establish easily after disturbance. Moreover, the dormant seeds persistent in soil make the control of ruderal weed species more challenging. Understanding the mechanisms of seed persistence of ruderal weed species in soil, particularly the relationship between seed dormancy and seed persistence will be essential for development of effective integrated weed management strategies.

1.4 OBJECTIVE OF THIS RESEARCH

The objective of this research is to examine the relationship between seed

dormancy and persistence of ruderal weed species in the SSB by a long-term burial study.

In this study, seeds of twelve ruderal species with various length of persistence in soil were used to determine the relationship between seed dormancy and persistence in soil: *Abutilon theophrasti* Medik. (velvetleaf), *Alliaria petiolata* (garlic mustard), *Amata tuberculatus* (common waterhemp), *Ambrosia trifida* L. (giant ragweed), *Chenopodium album* L.(common lambsquarters), *Ipomoea hederacea* (Ivyleaf morningglory), *Kochia scoparia* (L.) Schrad. (Kochia), *Panicum miliaceae* (wild proso millet), *Polygonum pensylvanicum* L. (Pennsylvania smartweed), *Setaria faberi* Herrm (giant foxtail), *Setaria lutescens* (L.) Beauv. (yellow foxtail), and *Thlaspi arvense* L. (field pennycress). The characteristics of these ruderal species were shown in Table 1.1.

The remainder of the dissertation is composed of 3 chapters. In Chapter 2 I will discuss the relationship between the seed dormancy and persistence of ruderal weed species in the soil seedbank. Chapter 3 summarizes the findings of this research. In chapter 4, the potential future directions of research are suggested.

Table 1.1 Some characteristics of twelve ruderal species

Species	Life history	Dormancy types [a]	Seed production (Seed/plant)	Half-life (year)	Resource
A. theophrasti	Annual	PY	7,800	8	(Schutte et al. 2010)
A. petiolata	Biannual	PD	323-710	NA [b]	(Rebek and O'Neil 2006, Sosnoskie and Cardina 2009)
A. tuberculatus	Annual	PD	~250,000	2	(Sellers et al. 2003, Leon and Owen 2006)
A. trifida	Annual	PD	10,300	<1/2	(Schutte et al. 2010)
C. album	Annual	PD	72,500	12	(Schutte et al. 2010)
I. hederacea	Annual	PY	5,800-6,000	<2	(Gomes et al. 1978, Crowley and Buchanan 1982, Holloway and Shaw 1995, Schutte et al. 2010)
K. scoparia	Annual	no dormancy	2,000 -30,000	<1/2	(Everitt et al. 1983, Dyer et al. 1993, Thompson et al. 1994, Stallings et al. 1995, Casey 2009)
P. miliaceae	Annual	PD	146-213	NA	(O'Tools 1983, Schutte et al. 2010)
P. pensylvanicum	Annual	NA	19,500	4	(Davis et al. 2005a)
S. faberi	Annual	PD	900	<1	(Baskin and Baskin 1998, Schutte et al. 2010)
S. lutescens	Annual	PD	6,500	5	(Dekker 2003, Davis et al. 2005a, Borza et al. 2007)
T. arvense	Annual	NA	15,000	6	(Moser et al. 2009)

a. Dormancy types: PD = physiological dormancy, PY = physics dormancy

b. NA = Not available

CHAPTER 2: RELATIONSHIP BETWEEN SEED DORMANCY AND PERSISTENCE OF SEEDS OF RUDERAL WEED SPECIES IN THE SOIL SEEDBANK

2.1 INTRODUCTION

SSBs are vital sources of recruitment but also critical to the persistence of annual weed species. The term "soil seedbank" refers to a reservoir of viable seeds on the surface of soil or in soil (Harper 1977, Roberts 1981, Simpson et al. 1989, Baskin and Baskin 1998). As a buffer against environmental uncertainty that leads to population decline or local extinction, SSBs exert important effects on population and community dynamics of annual weed species (Crawley 1997b, Rees 1997, Chesson 2000), thus persistent SSBs are important sources of weed species infestation and persistence (Cavers and Benoit 1989, Cavers et al. 1992, Warr et al. 1993, Cousens and Mortimer 1995, Davis 2006). Most annual weed species, including many of the world's most challenging weeds, have SSBs that allow them to maintain repeated infestation in arable lands (Holm et al. 1977, Booth et al. 2003). The reported weed seed densities in the arable soil range from a few hundred up to more than 150, 000 viable seeds m^{-2} (Forcella et al. 1992, Baskin and Baskin 2006). This large persistent SSB extends germination and emergence, and escapes from current weed control strategies, making weed management more challenging. Thus, reducing SSB persistence of weed species is an important goal of integrated weed management (Buhler 2002, Davis 2006).

A quantitative knowledge of seed persistence in soil can aid integrated weed management, both through identification of potential threats (e.g. species with especially

long persistence, whose seed return should be prevented as a management priority) and by assessing the relative impact of tactics that reduce inputs to the seedbank versus those that reduce recruitment from the seedbank (Mohler 2001). Seed persistence, the capability for a seed to remain the state of viable and non-geminated in soil for a period of time via various mechanisms (Thompson 2000, Walck et al. 2005), is closely related to seed longevity – the duration of a seed remaining viable (Murdoch and Ellis 2000). It has been used by botanists as a standard for classification of soil seedbanks (Thompson and Grime 1979, Grime 1981, Villiers et al. 2002, Csontos and Tamas 2003, Walck et al. 2005). For example, a functional seedbank classification system was established by separating SSBs into transient and persistent SSBs based on whether or not seeds remain viable in soil for more than one year (Thompson and Grime 1979, Grime 1981). In subsequent work, a five-year-threshold was applied to differentiate short-term versus long-term persistent soil seedbanks (Bakker et al. 1991, Thompson 1993, Bakker et al. 1996, Thompson et al. 1997, Walck et al. 2005). One common feature of these classification studies was the qualitative designation of persistence, which is not particularly useful for guiding weed management practices. The term half-life, the period of time to take for 50% of the initial seeds losing viability, reflects the potential length of a seed population can remain viable in soil (Roberts and Dawkins 1967, Thompson and Grime 1979, Auld 1986, Lutman et al. 2002, Ullrich et al. 2011). Because of the potential for continuous variation in seed half-life, I believe it is more practical to use quantitative measures of the seed persistence of a species in soil seedbank. Therefore, I used the half-life approach to quantify the seed persistence of annual species in soil in this study.

Quantifying persistence among species in a way that is consistent and predictable also involves consideration of main sources of variation and mechanisms affecting persistence. Seed persistence in SSBs varies among species (Buhler and Hartzler 2001); for example, some species such as *Setaria faberi* (giant foxtail) can only remain viable and non-germinate in soil less than one year (Davis et al. 2008), while seeds of *Abutilon theophrasti* (velvetleaf) can remain viable in soil as long as 39 years (Toole and Brown 1946). Knowledge related to seed persistence such as seed longevity, seed responses to the environment, proportion of seeds germinated in each year, timing of seedling emergence, etc. would be helpful for modeling prediction and final decision of weed control strategies (Forcella et al. 1993, Buhler et al. 1997, Wagner and Mitschunas 2008). Mechanistic understanding of the SSB persistence of weed species will improve the efficacy of integrated weed management systems.

Mechanisms that buffer weeds against uncertainty also help them escape management, but it is hard to identify which mechanisms are important. Successful establishment under unpredictable environmental conditions is critical for the persistence of plant species (Booth et al. 2003). For a given annual weed species, if the whole seed population germinates at the same time, that weed species would risk local extinction by a single disaster event, such as unfavorable weather conditions for either seed germination or seedling establishment, or destructive agricultural practices including tillage and weed control activities. Seed dormancy, the failure of an intact viable seed to complete germination under favorable conditions (Bewley 1997), is a 'bet-hedging' strategy used by annual weed species to maintain local populations under highly variable environments (Philippi 1993, Rees 1997, Booth et al. 2003, Fenner and Thompson 2005).

Weed seedling emergence fluctuates substantially across years and among species due to the dormancy level or release of dormancy (Forcella et al. 1992, Forcella et al. 1997). Many factors may influence the level and release of seed dormancy in soil. Among these factors, thermal conditions and water availability are of high importance and have received the greatest attention (Benech-Arnold et al. 2000, Koornneef et al. 2002, Allen et al. 2007). The environmental conditions prior to or right after seed dormancy release or the removal of constraints of germination are proposed to closely relate to seed dormancy. Most seeds of annual weeds are dispersed with primary dormancy, though the levels of dormancy vary among and within species. Formation of a dormant, persistent SSB may prevent seed germination under unfavorable conditions and wait for favorable conditions to germinate and successfully establish (Vleeshouwers et al. 1995, Benech-Arnold et al. 2000, Booth et al. 2003, Finkelstein et al. 2008). However, delaying germination through SSBs maximizes the overall fitness of the weed species at a cost to annual fitness. Between- and within-year variations in dormancy under variable environmental conditions may therefore promote the coexistence of multiple species via a "storage effect" which fosters niche differentiation through temporal variation of probability of germination (i.e. species in the SSB respond differently to the varying environments) (Chesson 2000, Mathias and Chesson 2013).

Although a relationship between seed dormancy and seed persistence in the SSB has been an underlying assumption of weed management in arable systems (hence the old farmers' saying, 'one year's seeding, seven year's weeding), the relationship between seed dormancy and seed persistence has not been adequately described from a quantitative standpoint. From the broader scientific literature on plant seedbank dynamics,

there is an existing strong claim that seed dormancy and seed persistence in soil are unrelated (Thompson et al. 2003). To support this argument, Thompson and his collaborators utilized a dataset derived from a very large, Europe-wide compendium of seed persistence data from many studies (Thompson et al. 1997, Thompson et al. 2003). Both seed dormancy and seed persistence were qualitatively determined in the dataset (Thompson et al. 1997). The dormancy of an individual species was characterized categorically, according to the various types of dormancy assigned in multiple studies, which did not imply any quantitative measurement of seed dormancy. Seed persistence was then described by a so called "longevity index" (Thompson et al. 1998). However, in the calculation of the longevity index, the persistence of all related species was only classified into transient (persistence less than one year) and persistent (persistence over one year). It did not differentiate the species forming short-term persistent and long-term persistent SSBs nor did it allow a quantitative comparison (Thompson et al. 1998). Because both the non-dormant seeds and long-term persistent SSB might be potentially categorized into either transient or persistent SSBs in different studies, the data collected from multiple studies easily run the risk of overestimating the persistence of non-dormant species and underestimating the persistence of species with different types of dormancy. Thompson et al. (2003) concluded that no relationship existed between seed dormancy and persistence in soil, based upon their analysis of a numerical seed persistence index derived from qualitative seedbank data. I do not believe that this approach adequately supported the authors' strong claim about the lack of relationship between seed dormancy and persistence. Quantitative estimates of both seed dormancy and persistence would be needed to test the hypothesis more effectively.

In the present study, my objectives were to (1) quantify the relationship between seed dormancy and persistence in seedbanks of ruderal weed species, and (2) determine whether variation in dormancy is also related to seed persistence for this group of plants. Results from the first objective will indicate whether seed dormancy might be a useful predictor of seed persistence for ruderal weed species in soil. The second will clarify the degree to which extrinsic or intrinsic mechanisms involved in the release of seeds from dormancy affect seed persistence.

I hypothesized that if seed dormancy and seed mortality operate independently, seed dormancy should constitute a "bet-hedging strategy" that increases seed persistence in soil, such that there should be a positive linear relationship between seed dormancy and seed persistence of ruderal weed species. In the SSB of any given ruderal weed species, the dynamics of the persistent seeds can be described by equation 1 (Cousens and Mortimer 1995):

$$N_t = N_{t-1} - g - d + b \qquad (1)$$

where N_t and N_{t-1} are the number of viable seeds in the SSB at time points *t* and *t-1*, respectively; *g*, *d*, and *b* represent seedlings emerging from soil, seed death, and seed of the specific ruderal weed species added to the SSB between time *t-1* and *t*, respectively. This expectation is based on the assumption that seed dormancy and mortality are independent.

In equation 1, when N_t declines to as low as zero, the entire SSB of the given species depletes from the soil. It is not persistent any more. In my experimental system, no new seeds were added every year. Therefore, under the assumption that increased dormancy should not lead to increased seed death, if there is a high number of dormant

seed, I would expect few emerging seedlings between time *t-1* and *t* for the given weed species.

Predicting the relationship between variation in dormancy and seedbank persistence is less straightforward. I hypothesized that if variation in dormancy release across years is related primarily to extrinsic environmental conditions; there should be a positive relationship between dormancy variance and seedbank persistence of annual weed species. If dormancy release in a species is under extrinsic control, then 'choosy' species that accept only a narrow set of conditions for stimulation of germination should exhibit a wider variance of dormancy across years varying in environmental conditions. Species with less stringent criteria for dormancy release (which allow seeds to germinate across a wider range of conditions) should have a comparatively narrow set of dormancy levels over time, with lower variance in dormancy (Bewley 1997, Benech-Arnold et al. 2000, Koornneef et al. 2002, Allen et al. 2007). If a more constant fraction of seeds is germinating over time, then I would expect the seeds of such a species to be depleted from the seedbank more quickly, with lower observed half-lives in the SSB, than those of a species that releases its seeds less readily from dormancy (based on the hypothesis of seed dormancy not related to seed death).

2.2 MATERIALS AND METHODS

Eleven annual weed species and one biennial invasive with a wide range of seed half-lives reported in the scientific literature (Lueschen et al. 1993, Burnside et al. 1996, Buhler and Hartzler 2001, Evans et al. 2012) were included in the seed burial study: *Abutilon theophrasti* Medik. (velvetleaf), *Alliaria petiolata* (garlic mustard), *Amata*

tuberculatus (common waterhemp), *Ambrosia trifida* L. (giant ragweed), *Chenopodium album* L. (common lambsquarters), *Ipomoea hederacea* (ivy leaf morningglory), *Kochia scoparia* (L.) Schrad. (Kochia), *Panicum miliaceae* (proso millet), *Polygonum pensylvanicum* L. (Pennsylvania smartweed), *Setaria faberi Herrm* (giant foxtail), *Setaria lutescens* (L.) Beauv. (yellow foxtail), and *Thlaspi arvense* L. (field pennycress).

Seed collection. Seeds of all study species were collected from University of Illinois field plots (arable weeds) and adjoining wood lot (*A. petiolata*) during the 2007 growing season in Savoy, Illinois, USA (40.048000N, – 88.236489W). For each species, mature seeds were collected at the time of seed dehiscence by gently shaking the inflorescences of 50 mother plants from within contiguous patches no larger than 10 m in diameter into a large paper bag. Seeds were allowed to air dry in open paper bags for three weeks at 25 ˚C before storing in air tight plastic containers at 4 ˚C prior to use.

Experimental design and seed burial. Seeds were buried in a single field plot at the same research farm from which they were collected. The soil at the study site was a Catlin silt loam (Oxyaquic Argiudoll) with 7% sand, 68% silt, 25% clay, pH 7.2, and 4.2% soil organic carbon. Experimental units were arranged within the 4 x 10 m seed burial site in a split-plot randomized complete block design (RCBD) with four replications of *recovery year* (main plot: 5 levels, 2008 through 2012) and *species* (split plot, consisting of the 12 species mentioned above).

Each replicate experimental unit contained twelve seed burial units, randomized by species. Seed burial units consisted of a 10 cm by 10 cm by 4 cm deep wire mesh tray with 0.5 mm openings. In each burial unit, to a depth of 3 cm, 100 seeds of a given species were mixed with field soil collected from underneath a long-term grass sward

with negligible seed population densities of the study species. Prior to burial, seed viability was tested via tetrazolium staining (Peters 2000). Seed burial units were placed in the field on 15 October, 2007. Each experimental unit was covered with a 35 cm x 45 cm wire mesh rectangle with 1 cm openings to allow access to invertebrate seed predators, but to deter larger vertebrates from disturbing the burial units. The entire burial plot was surrounded with a 1 m high fence to exclude large vertebrates.

During each growing season, seedlings emerging from mesh trays were counted and removed. Seeds were retrieved from mesh trays in October of the pre-assigned recovery year for that experimental unit. Intact seeds were recovered from soil through hand-elutriation, followed by a two-stage viability testing procedure. First the recovered seeds from each basket were placed on moist filter paper in petri dishes for 96 hr under 12 hr dark/light cycles at 15 ˚C dark/25 ˚C light, to assay for readily germinable seeds (quiescent seeds). In all cases, seed germination was nil, indicating that recovered seeds were dormant. Following this, viability of the retrieved dormant seeds was determined through tetrazolium testing.

Seedbank persistence. Based on an assumption that seed undergoes seed decay at a constant rate across years for a given weed species and follows a negative exponential curve (Roberts and Dawkins 1967, Thompson and Grime 1979, Grenz et al. 2005, Conn et al. 2006), half-lives of seeds of the twelve weed species in the SSB were calculated using nonlinear least-squares regression by relating the proportion of the initial seed pool to seed burial time for each of these species (Davis et al. 2008). A negative exponential function $y = ae^{-kt}$, where a refers to the initial proportion of viable seed in seedbank and k is the constant representing the decay rate for the given species, was fit to the data in the

nlme package of R (version 2.13.1) (R Foundation for Statistical Computing 2010). Seed half-life ($t_{0.5}$) in the SSB for each of these species was calculated as $t_{0.5} = \ln(0.5/a)/(-k)$ (Davis et al. 2008).

Environmental data. The microclimate at the depth of three centimeters was simulated using the Soil Temperature and Moisture Model (STM^2) (Spokas et al. 2007, Schutte et al. 2008c) with weather data at South Farms obtained for the relevant period (2007 to 2012) from NCDC (National Climate Data Center: http://www.ncdc.noaa.gov/cdo-web/) including latitude, longitude, elevation, daily precipitation, daily air minimum temperature, and daily maximum air temperature. The consequent simulated average daily soil temperature and soil matric potential (SMP) were used to calculate average soil temperature and SMP and variance of soil temperatures and SMP from October of previous year to March and from March to June over the burial course.

*Statistical analyses***.** The number of dead seeds (*d*) between year *t* and year *t+1* was calculated by subtracting the number of seedlings (*g*) removed during the growing season and the number of viable seeds (N_{t+1}) at year *t+1* from the number of viable seeds (N_t) at year *t* determined by TZ test in October of each year (equation 2). The proportion of emerged seeds (*g%*) between year *t* and *t+1* was calculated by dividing the number of seedlings (*g*) with the difference between viable seeds (N_t) in year *t* and dead seeds (*d*) between two years (equation 3). Then the proportion of dormant seeds (*dorm%*) at the beginning of year *t* was 1- the proportion of emerged seeds (*g%*) between year *t* and *t+1* (equation 4). The proportion of persistent seeds (*pers%*) in year *t+1* was calculated by dividing the number of viable seeds (N_{t+1}) determined by TZ test in October of year *t+1* with the number of initial viable seeds (N_0) (equation 5).

$$d = N_t - N_{t+1} - g \quad (2)$$

$$g\% = \frac{g}{N_t - d} \times 100\% \quad (3)$$

$$dorm\% = 1 - g\% \quad (4)$$

$$pers\ \% = \frac{N_{t+1}}{N_0} \times 100\% \quad (5)$$

The dynamics of seed persistence was fit to a negative exponential model with the self-starting nonlinear function SSasymp in the *nlme* package of R. The full nonlinear mixed effects model for seed persistence over time contained terms for fixed (recovery year, species) and random (replicate) effects. The linear regression analyses between seed dormancy and half-lives and between seed dormancy (asin(x ^ 0.5) transformed) and the environmental conditions were conducted in the package of stats in R. The assumptions (normality and homogenous variance) for the linear regression were checked prior to the regression analysis. The nonlinear least-square regression analysis between variance of dormancy and half-lives was done with a function SSasymp in the package of *nlme* in R. All analyses were performed in R v. 2.13.1 (R Foundation for Statistical Computing 2010).

2.3 RESULTS

The dynamics of seed persistence of the twelve species were described well by the negative exponential function (Figure 1). Visual inspection of the fitted curves indicated low within-year variation in seed persistence over the burial course for species *K. scoparia*, *P. pensylvanicum*, *S. lutescens*, and *T. arvense*, low within-year variations of

seed persistence in first two years and high variations of seed persistence in last three years for species *A. petiolata* and *P. miliaceae,* and high within-year variations of seed persistence over the burial courses of other species. The slopes of the curves varied with highest steepness for species *K. scoparia and A. petiolata* and lowest steepness for the species *A. theophrasti* and *C. album* (Figure1). For all twelve ruderal weed species, seed persistence dramatically dropped during the 1st year of burial. Especially, there were no seed of *K. scoparia* and *A. petiolata* remained persistent after one year burial (Figure 1). The percent of seed persistence of *S. lutescens* and *T. arvense* dropped to about 0 at the end of 2nd year. There were about less than 10% of seeds of weed species *A. trifida, P. miliaceae, P. pensylvanicum,* and *S. faberi* remained as persistent seeds, while seed persistence of *A. theophrasti, A. tuberculatus, C. album,* and *I. hederacea* lasted longer than the other species (Figure 1). Therefore, the dynamics of seed persistence of ruderal weed species followed a negative exponential curve and within-year variations in seed persistence, steepness of slopes, and remaining proportions of persistent seed varied.

The half-lives of the twelve weed species ranged from 0.25 to 2.22 years (Table 1). Mixed model analysis indicated a significant main effect of species on half-life ($F_{11, 33} = 15.9$, $P < 0.0001$). Among the twelve ruderal weed species, the half-lives of three species, *A. theophrasti, C. album,* and *A. tuberculatus,* were longer than 1.5 years. The half-lives of six species: *I. hederacea, S. lutescens, P. miliaceae, S. faberi, A. trifida,* and *P. pensylvanicum* were between 0.5 and 1.5 years. The half-lives of the remaining three species *K. scoparia, A. petiolata,* and *T. arvense* were shorter than 0.5 years.

Regression analysis between the average dormancy over burial time course and half-lives of the 12 ruderal weed species indicated that there is a significant positive

relationship between seed dormancy and half-life (Figure 2A, slope = 0.05, $p < 0.001$, $R^2 = 0.92$). There was also a significant negative nonlinear relationship between the variance of seed dormancy and half-life (the three parameters for nonlinear model *a*, *b*, and *c* were 0.43, 2.14, and -5.21 respectively, with all *p* values less than 0.05) (Figure 2B). For the three least persistent species *K. scoparia*, *A. petiolata*, and *T. arvense*, their half-lives and average proportions of dormancy were similar, but their variance of dormancy over the burial courses were quite different (Figure 2A and 2B). The variance of dormancy of *S. faberi* is different from other species with intermediate persistence (Figure 2B). The above two regression analyses demonstrated that there is a strongly positive relationship between seed dormancy and persistence, but negative relationship between variance of seed dormancy and persistence of ruderal weed species in soil.

Out of 96 regression analyses between seed dormancy and average soil temperature and soil matric potential (SMP) or between seed dormancy and the variance of soil temperature and SMP from October in previous year to March, and March to June, only one was significant (Appendix Table A1 and Table A2). This indicates no support for significant effects of environmental conditions on inter-annual variation in seed dormancy for these species.

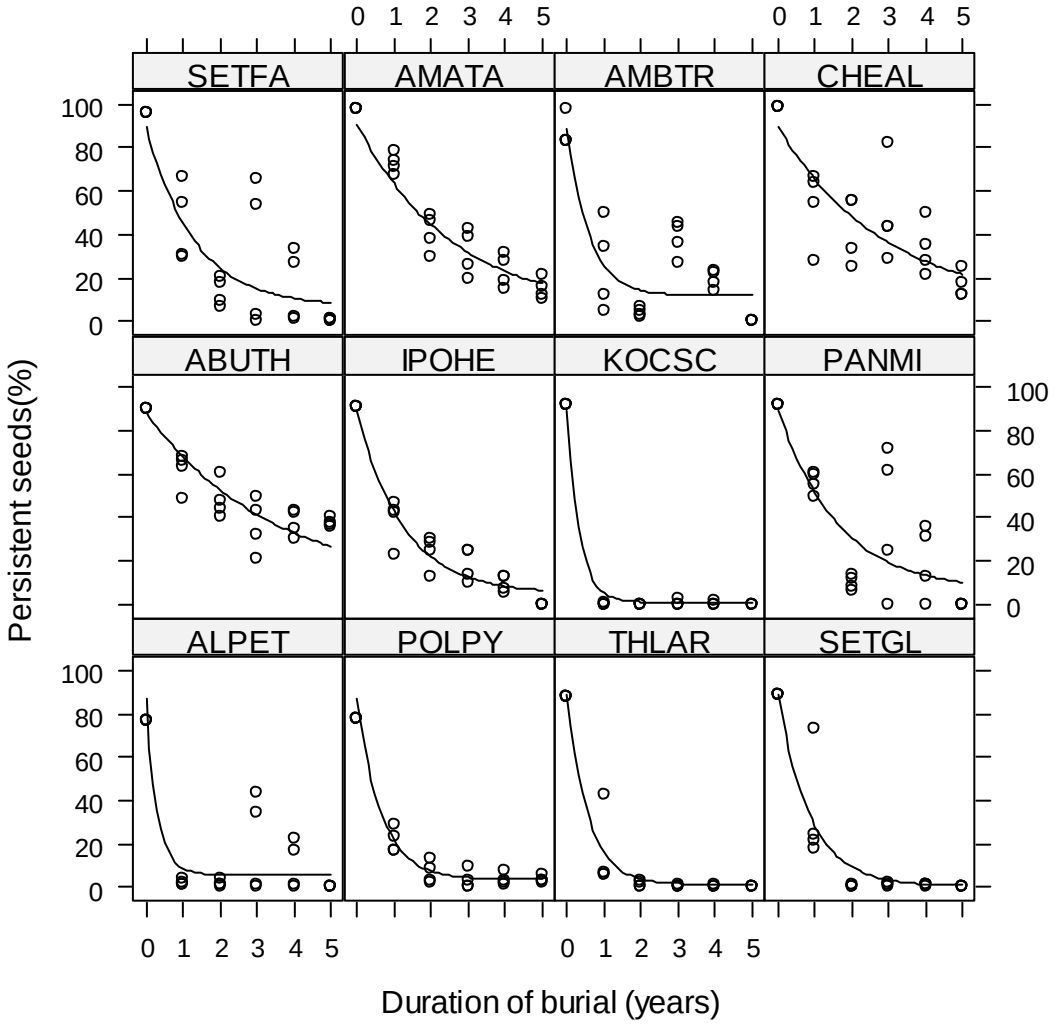

Figure 2.1 The dynamics of seed persistence over burial course from October 2007 to October 2012 of the twelve ruderal weed species in Savoy, IL. Solid lines represent the predicted trends of the twelve species. The percentage of persistent seeds was calculated based on the original number of viable seeds at the beginning of the burial course (October 2007). Each panel represent dynamics of seed persistence for a specific species, where ABUTH = *A. theophrasti*, ALPET = *A. petiolata*, AMATA = *A. tuberculatus*, AMBTR = *A. trifida*, CHEAL = *C. album*, IPOHE = *I. hederacea*, KOCSC = *K. scoparia*, PANMI = *P. miliaceae*, POLPY = *P. pensylvanicum*, SETFA = *S. faberi*, SETLU = *S. lutescens*, and THLAR = *T. arvense*.

Table 2.1 Half-lives (mean of 12 ± se, n = 4) of twelve ruderal weed species. Following formula was used to calculate half-life: $t_{0.5}$ = (ln ((50 - *asym*) / (c_0 - *asym*))) / (- exp (*lrc*)). *Asym*, c_0, and *lrc* are three parameters calculated from the nonlinear model (nlm) with the formula of $y = asym + (c_0 - asym) * \exp(-\exp(lrc) * t)$, where *t* is the time of burial, and *y* is the percentage of persistence calculated by dividing the sum of total number viable seeds according to TZ test and the number of germinated seeds in the growing seasons by the number of viable seeds of each burial unit at the beginning of the burial.

Species	**Half-lives (Years)**
A. theophrasti	2.22 ± 0.25
A. petiolata	0.27 ± 0.01
A. tuberculatus	1.65 ± 0.13
A. trifida	0.60 ± 0.17
C. album	1.94 ± 0.43
I. hederacea	0.82 ± 0.09
K. scoparia	0.25 ± 0.00
P. miliaceae	1.16 ± 0.22
P. pensylvanicum	0.43 ± 0.02
S. faberi	1.00 ± 0.23
S.lutescens	0.50 ± 0.10
T. arvense	0.36 ± 0.07

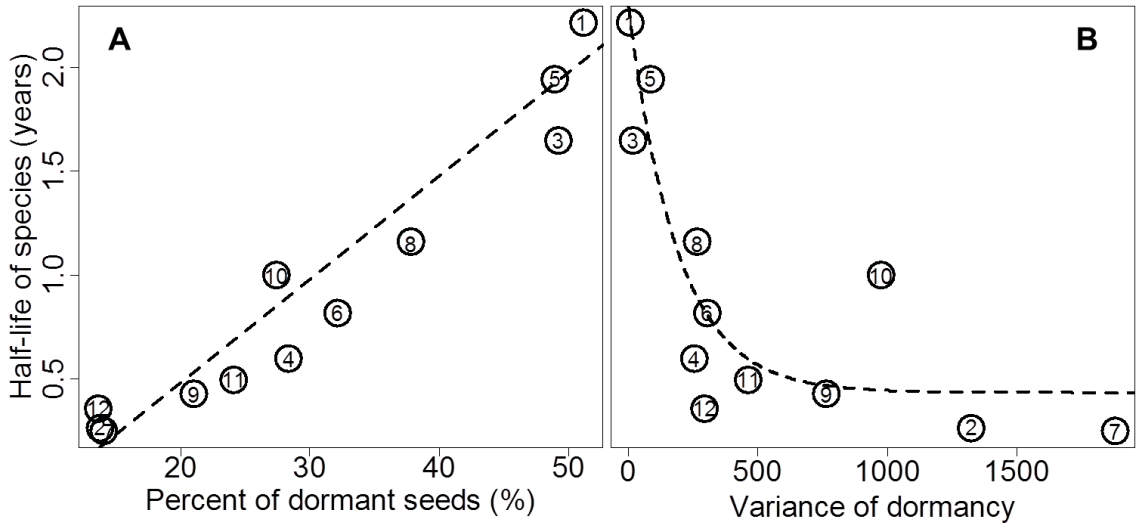

Figure 2.2 Seedbank persistence (half-life) in relation to seed dormancy (A) and variance in seed dormancy over the burial period (B). Half-lives were calculated for each individual species based on the percent of persistent seed in relation to the initial number of viable seeds at the beginning of the burial course (October, 2007). In plot A, the symbols are means of the percentage of dormant seeds over five years. Open cycles in each figure represent twelve species respectively, where 1 = *A. theophrasti*, 2 = *A. petiolata*, 3 = *A. tuberculatus*, 4 = *A. trifida*, 5 = *C. album*, 6 = *I. hederacea*, 7 = *K. scoparia*, 8 = *P. miliaceae*, 9 = *P. pensylvanicum*, 10 = *S. faberi*, 11 = *S. lutescens*, and 12 = *T. arvense*.

2.4 DISCUSSION

Strong positive correlation between seed dormancy and half-lives of twelve ruderal weed species suggests a positive relationship between seed dormancy and persistence of ruderal weed species in soil. This supports my original prediction regarding the relationship between seed dormancy and persistence of ruderal weed species in soil and thus provides evidence that seed dormancy provides a "bet-hedging" strategy that increases seed persistence of ruderal weed species in soil. This result does not support the claim of Thompson et al. (2003) that no relationship exists between seed dormancy and seed persistence in soil. The dynamics of seed persistence of all twelve weed species follow a negative exponential function (Roberts and Dawkins 1967, Thompson and Grime 1979, Grenz et al. 2005, Davis et al. 2008, Ullrich et al. 2011) and, thus provide a rationale for the calculation of half-lives. In contrast to the persistence index (Thompson et al. 1998, Thompson et al. 2003), half-lives reflect the quantitative dynamics of seed persistence of different species so that they can provide a better and useful understanding of the seed persistence in soil than the qualitative persistence index. In this research, I constrained my research targets in a specific group of plants – eleven ruderal annuals and one biennial invasive, rather than a large dataset from multiple studies. My experiment was also conducted under a smaller range of environmental conditions than that of Thompson et al. (2003). While the smaller group of species and narrower environmental range helped generate a dataset suitable for testing the relationship between seed dormancy and persistence, it also clearly limits my ability to extrapolate from this experiment to the broader set of seedbank forming plants across a

range of environments. Further empirical work is needed to quantitatively test this relationship for a wider range of species and environments.

Dormancy release of the seeds of ruderal weed species was not dominated by extrinsic control. The negative relationship between variance of seed dormancy and half-lives contrasted with my original prediction of a positive relationship between the variance of seed dormancy and persistence in soil of ruderal weed species. Meanwhile, no significant relationship between seed dormancy and environmental conditions were detected. Both of these results indicate that inter-annual variation in dormancy release of the seeds of ruderal weed species is not under strong extrinsic control. It appears instead that dormancy release of the seeds of ruderal weed species may be under some form of intrinsic control. A common garden approach, coupled with seeds collected from different genotypes of multiple species, may be used in future studies to determine the degree to which dormancy release of seeds of ruderal weed species is under intrinsic control.

The significant species effects on half-lives and intrinsic control of dormancy release indicate that there is substantial diversity in seed dormancy. As in other areas of plant ecology, one of the driving questions of seedbank ecology is what maintains diversity of traits in SSB communities. Surviving under unfavorable conditions as dormant seeds in the soil is a potential strategy for annual species to increase their fitness (Crawley 1997a). High diversity of seed dormancy in soil may stimulate the coexistence of multiple weed species via the storage effect (Chesson and Warner 1981, Facelli et al. 2005, Sears and Chesson 2007, Mathias and Chesson 2013). The high diversity of seed dormancy, both at the level of mean and variance, may be due to either direct natural

selection on this trait -- seed dormancy as a driver of change, or from natural selection on other plant traits related to seed dormancy -- seed dormancy as an evolutionary hitchhiker. As an example of the latter mechanism, population-level variation in seed dormancy in the genus *Setaria* appears to arise from seed position on the maternal plant (Dekker et al. 1996); therefore, morphological differences among plant species in their reproductive structures could potentially contribute to species-level differences in the variance of dormancy. Some other factors may favor maintenance of genetic diversity in weed community as well, such as field operations, sources allocation, and predation, safe sites in soil, seed polymorphisms, and dispersal away from parent plants with multiple external seed structural equipment to ensure different dispersal distances (Crawley 1997a, Booth et al. 2003). For example, plants of *C. album* may produce dimorphic, black and brown, seeds. The brown seeds are larger, non-dormant and germinate rapidly to a high proportion at a wider range of environmental conditions, while most of the black seeds are dormant (Yao et al. 2010). This highlights the need to study the strategies for weed species to maintain dormancy diversity for weed management.

Even though seed persistence is an important characteristic of the SSB, it remains a challenge to determine the persistence of seeds in the soil seedbank. Long term burial studies are commonly used to determine seed longevity of different species in soil, but they are time consuming and expensive to maintain (Toole and Brown 1946, Roberts and Dawkins 1967, Lewis 1973, Lueschen and Andersen 1980, Zorner et al. 1984, Burnside et al. 1996, Telewski and Zeevaart 2002, Conn and Werdin-Pfisterer 2010). For example, the first famous seed burial study initiated by Dr. W. J. Beal in East Lansing, Michigan in 1879 lasted more than 120 years (Darlington 1922, 1931, 1941, 1951, Darlington and

Steinbauer 1961, Kivilaan and Bandurski 1973, 1981, Telewski and Zeevaart 2002). Another famous seed burial study initiated by J. T. Duvel was discontinued after 39 years (Toole and Brown 1946). The data availability on seed persistence of reported weed species (8,000 species according to Holm et al. (1977) are limited due to the cost and time consuming nature of seed burial study. The positive relationship between seed dormancy and persistence that I found suggests that weed species with higher dormancy may be associated with longer persistence in the soil seedbank. Therefore, the positive linear relationship between seed dormancy and persistent may be useful for predicting seed persistence of ruderal weed species. The application of data on seed dormancy to predict seed persistence of weed species may contribute to speeding up the process of seed persistence assessment to facilitate weed seedbank management strategies. However, this conclusion on the relationship of seed dormancy and seedbank persistence is only based on a small set of data. More research on ruderal species from other habitats or species with different life histories is needed.

One result of this study with great importance to weed management was not part of the original objectives. The half-lives of seeds in the SSB estimated from seed persistence data are considerably lower than those reported in other studies (Lueschen et al. 1993, Burnside et al. 1996). The shorter seed persistence of even the most persistent species implies that seedbank management may be a more realistic option for weed management than previously thought. For example, the half-life of *C. album* was found to be about 1.94 years in this study which is much shorter than that obtained from Burnside et al.'s study (Burnside et al. 1996, Davis et al. 2008). Another study reported that seeds of *C. album* were still available after burial of 39 years. The half-lives of seeds of *A.*

theophrasti is only one fourth, *S. lutescens* is only one ninth, and *T. arvense* one tenth of those obtained from other studies (8.3, 4.5, and 3.5 years respectively) (Lueschen et al. 1993, Burnside et al. 1996, Davis et al. 2008). The half-life of *S. faberi* is slightly longer than that reported by Buhler and Hartzler (2001) and the half-life of *K. scoparia* in my study is similar to that from Burnside et al's study (Burnside et al. 1996). Such results may provide an added incentive to farmers to manage weed seedbanks rather than be dismayed at the very long time frames previously thought to be necessary to deplete soil seedbanks.

The difference in half-lives found among studies is probably due to different environmental conditions. In Burnside et al's study, the seeds of different species were buried in plastic containers at a depth of 20 cm in soil in Western Nebraska (Burnside et al. 1996). The enclosed burial environment and deeper burial placement likely reduced losses of seeds to decay, germination and seed predation, compared to this study. Shallow burial of seed increases the opportunity of seed exposing to light, soil aeration, and more frequent temperature fluctuation and thus, stimulate seed depletion from SSB via germination. Seed losses resulting from germination (Baskin and Baskin 1998, Arrieta and Suarez 2004), predation (Lerner and Peinetti 1996, Hulme 1998, Harrison and Regnier 2003, Menalled et al. 2006, Davis et al. 2008, Davis and Raghu 2010, Dalling et al. 2011), pathogens (Crist and Friese 1993, Kremer 1993, Lonsdale 1993, Chee-Sanford 2008, Wagner and Mitschunas 2008, Fuerst et al. 2011), and aging (Priestley 1986) are the major causes of seed persistence reduction in soil. Besides the features of seed per se, the maternal conditions (Schutte et al. 2008a), burial depth (Davis and Renner 2007), burial site environmental conditions (Schutte et al. 2008a), and the agricultural practices

(Cardina et al. 1991, Mulugeta and Stoltenberg 1997, Cardina et al. 2002, Gallandt et al. 2004, Conn 2006, Gruber et al. 2010, Mirsky et al. 2010) may also influence persistence of seeds in the soil seedbank.

The variation of seed persistence under different environmental conditions and management systems is an important consideration for producers wishing to reduce their reliance upon herbicides for weed management. For weed species with seeds that have low half-lives in the SSB, there is a high potential to deplete the SSB through manipulation of seed dormancy, while for long-persistent species, strategies involving approaches to prevent new input of seed into soil would be encouraged. For example, the "stale seedbed" would be a suitable approach to deplete SSB of these weed species (Liebman et al. 2001). The results presented here contribute to the scientific basis for SSB management as an important component of integrated weed management, pointing to the importance of flexible depletion strategies ranging from dormancy manipulation to weed seed rain prevention. Perhaps more importantly, these results indicate that weed seedbank depletion is feasible, due to lower seed half-lives than previously reported.

CHAPTER 3: SUMMARY AND CONCLUSIONS

This study quantified the relationship between seed dormancy and persistence of ruderal species in SSB and determined whether variation in dormancy is also related to seed persistence for this group of plants. The findings of this study were summarized as following:

Seed dormancy is positively related to seed half-life ($t_{0.5}$). This result indicates a strong relationship between the dormancy and persistence of seeds of ruderal weed species in the soil seedbank. This means a seed population with lower seed dormancy would be associated with lower persistence and thus, there is a high possibility to deplete the SSB through manipulation of seed dormancy. Therefore, this implies that seed dormancy might be a useful predictor of seed persistence for ruderal weed species in soil.

Seed half-lives of the twelve ruderal species in SSB ranged from 0.25 to 2.22 years, considerably shorter than other reports of $t_{0.5}$ for the same weed species. The shorter seed persistence of even the most persistent species implies that seedbank management may be a more realistic option for weed management than previously thought. Applying the prediction function of the positive relationship between seed dormancy and persistence and seedbank depletion approaches may help make management of weed SSBs more feasible.

Considered together, the negative nonlinear relationship between variance of seed dormancy and $t_{0.5}$ and lack of relationship between environmental conditions during the course of seed burial and seed dormancy across study years indicate that dormancy release for these species was at least partially controlled by intrinsic seed characteristics.

There was substantial species-level diversity in seed dormancy. High diversity of seed dormancy in SSBs may support the coexistence of multiple weed species through complementary bet-hedging strategies. Whereas some species with low seed dormancy may exploit suitable safe-sites for recruitment at shorter time scales, other species with greater seed dormancy may be holding a greater proportion of their buried seed in reserve for lower-frequency, higher quality recruitment opportunities, resulting in replenishment of the soil seedbank.

CHAPTER 4: FUTURE RESEARCH NEEDS

Based on the results of my dissertation work, I believe that the following topics deserve further study in the future:

First, this study demonstrates that seed dormancy is positively related to seed persistence of ruderal species in soil. This finding does not support Thompson et al.'s statement that seed dormancy and seed persistence are not related (Thompson 2000, Thompson et al. 2003). However, the scope of this study was limited, with a small group of ruderal species and narrow environmental range. To enhance our ability to extend the conclusion from this experiment to the broader set of seedbank forming plants across a range of environments, further empirical work is needed to quantitatively test this relationship for a wider range of species and environments. Meanwhile, the dormancy of seeds used in this study encompasses multiple dormancy types. Whether this relationship would be true within a unique type of seed dormancy is also of interest.

Second, the positive relationship between seed dormancy and persistence of ruderal species also suggests the possibility to use the positive relationship between seed dormancy and persistence to predict the SSB persistence of specific weed species. More research should be done on the feasibility of using this relationship to predict seed persistence across species and guide weed management practice.

Third, the results of this study suggest that dormancy release for these species was at least partially controlled by intrinsic seed characteristics. A well designed common garden approach with species of multiple genotypes in multiple locations is needed to test this hypothesis.

Finally, the shorter seed persistence of even the most persistent species found in this study implies that seedbank management may be a more realistic option for weed management. Future research efforts focusing on reduction of persistence of SSBs or depletion of SSBs would therefore have high relevance to improving ecological weed management options.

REFERENCES

Allen, P. S., R. L. Benech-Arnold, D. Batlla, and K. J. Bradford. 2007. Modeling of seed dormancy. Pages 72-112 Annual Plant Reviews Volume 27: Seed Development, Dormancy and Germination. Blackwell Publishing Ltd.

An, S. Q., B. H. Gu, C. F. Zhou, Z. S. Wang, Z. F. Deng, Y. B. Zhi, H. L. Li, L. Chen, D. H. Yu, and Y. H. Liu. 2007. *Spartina* invasion in China: implications for invasive species management and future research. Weed Research **47**:183-191.

Arrieta, S. and F. Suarez. 2004. Germination and seed bank depletion of holly (*Ilex aquifolium* L.) in four microhabitat types. Seed Science Research **14**:305-313.

Auld, T. D. 1986. Population dynamics of the shrub *Acacia suaveolens* (Sm.) Willd: dispersal and the dynamics of the soil seed-bank. Australian Journal of Ecology **11**:235-254.

Baig, M. N. 1992. Natural revegetation of coal-mine spoils in the rocky-mountains of Alberta and its significance for species selection in land restoration. Mountain Research and Development **12**:285-300.

Bakker, J. and F. Berendse. 1999. Constraints in the restoration of ecological diversity in grassland and heathland communities. Trends in Ecology & Evolution **14**:63-68.

Bakker, J. P., A. F. Bos, J. Hoogveld, and H. J. Muller. 1991. The role of the seed bank in restoration management of semi-natural grasslands. *In* O. Ravera, editor. Terrestrial and Aquatic Ecosystems: Perturbation and Recovery. Ellis Horwood, New York.

Bakker, J. P., P. Poschlod, R. J. Strykstra, R. M. Bekker, and K. Thompson. 1996. Seed bank and seed dispersal: important topics in restoration ecology. Acta Botanica Neerlandica **45**:461-490.

Baskin, C. C. and J. M. Baskin. 1998. Seeds: Ecology, Biogeography, and Evolution of Dormancy and Germination. Academic Press, San Diego.

Baskin, C. C. and J. M. Baskin. 2006. The natural history of soil seed banks of arable land. Weed Science **54**:549-557.

Baskin, J. M. and C. C. Baskin. 2004. A classification system for seed dormancy. Seed Science Research **14**:1-16.

Bekker, R. M., J. P. Bakker, U. Grandin, R. Kalamees, P. Milberg, P. Poschlod, K. Thompson, and J. H. Willems. 1998. Seed size, shape and vertical distribution in the soil: indicators of seed longevity. Functional Ecology **12**:834-842.

Benech-Arnold, R. L., R. A. Sánchez, F. Forcella, B. C. Kruk, and C. M. Ghersa. 2000. Environmental control of dormancy in weed seed banks in soil. Field Crops Research **67**:105-122.

Bernhardt, K. G., M. Koch, M. Kropf, E. Ulbel, and J. Webhofer. 2008. Comparison of two methods characterising the seed bank of amphibious plants in submerged sediments. Aquatic Botany **88**:171-177.

Bewley, J. D. 1997. Seed germination and dormancy. Plant Cell **9**:1055-1066.

Booth, B. D., S. D. Murphy, and C. J. Swanton. 2003. Weed Ecology: in Natural and Agricultural Systems. CABI Publishing.

Borza, J. K., P. R. Westerman, and M. Liebman. 2007. Comparing estimates of seed viability in three foxtail (*Setaria*) species using the imbibed seed crush test with and without additional tetrazolium testing. Weed Technology **21**:518-522.

Bossuyt, B. and M. Hermy. 2001. Influence of land use history on seed banks in European temperate forest ecosystems: a review. Ecography **24**:225-238.

Brown, D. 1992. Estimating the composition of a forest seed bank: a comparison of the seed extraction and seedling emergence methods. Canadian Journal of Botany **70**:1603-1612.

Buhler, D. D. 2002. Challenges and opportunities for integrated weed management. Weed Science **50**:273-280.

Buhler, D. D. and R. G. Hartzler. 2001. Emergence and persistence of seed of velvetleaf, common waterhemp, woolly cupgrass, and giant foxtail. Weed Science **49**:230-235.

Buhler, D. D., R. G. Hartzler, and F. Forcella. 1997. Implications of weed seedbank dynamics to weed management. Weed Science **45**:329-336.

Buhler, D. D. and B. D. Maxwell. 1993. Seed separation and enumeration from soil using K_2CO_3-centrifugation and image analysis. Weed Science **41**:298-302.

Burnside, O. C., R. G. Wilson, S. Weisberg, and K. G. Hubbard. 1996. Seed longevity of 41 weed species buried 17 years in Eastern and Western Nebraska. Weed Science **44**:74-86.

Cao, M., Y. Tang, C. Sheng, and J. Zhang. 2000. Viable seeds buried in the tropical forest soils of Xishuangbanna, SW China. Seed Science Research **10**:255-264.

Cardina, J., C. P. Herms, and D. J. Doohan. 2002. Crop rotation and tillage system effects on weed seedbanks. Weed Science **50**:448-460.

Cardina, J., E. Regnier, and K. Harrison. 1991. Long-term tillage effects on seed banks in three Ohio soils. Weed Science **39**:186-194.

Cardina, J. and D. H. Sparrow. 1996. A comparison of methods to predict weed seedling populations from the soil seedbank. Weed Science **44**:46-51.

Carrick, P. J. and R. Kruger. 2007. Restoring degraded landscapes in lowland Namaqualand: lessons from the mining experience and from regional ecological dynamics. Journal of Arid Environments **70**:767-781.

Casey, P. A. 2009. Plant guide for kochia (*Kochia scoparia*). USDA-Natural Resources Conservation Service, Kansas Plant Materials Center. Manhattan, Kansas.

Cavers, P. B. and D. L. Benoit. 1989. Seed banks in arable land. *In* M. A. Leck, V. T. Parker, and R. L. Simpson, editors. Ecology of Soil Seed Banks. Academic Press, San Diego.

Cavers, P. B., M. Kane, and J. J. Otoole. 1992. Importance of seedbanks for establishment of newly introduced weeds - a case-study of proso millet (*Panicum-miliaceum*). Weed Science **40**:630-635.

Chee-Sanford, J. C. 2008. Weed seeds as nutritional resources for soil Ascomycota and characterization of specific associations between plant and fungal species. Biology and Fertility of Soils **44**:763-771.

Chee-Sanford, J. C., M. M. Williams, A. S. Davis, and G. K. Sims. 2006. Do microorganisms influence seed-bank dynamics? Weed Science **54**:575-587.

Chesson, P. 2000. Mechanisms of maintenance of species diversity. Annual Review of Ecology and Systematics **31**:343-366.

Chesson, P. L. and R. R. Warner. 1981. Environmental variability promotes coexistence in lottery competitive systems. The American Naturalist **117**:923-943.

Conn, J. S. 2006. Weed seed bank affected by tillage intensity for barley in Alaska. Soil and Tillage Research **90**:156-161.

Conn, J. S., K. L. Beattie, and A. Blanchard. 2006. Seed viability and dormancy of 17 weed species after 19.7 years of burial in Alaska. Weed Science **54**:464-470.

Conn, J. S. and N. R. Werdin-Pfisterer. 2010. Variation in seed viability and dormancy of 17 weed species after 24.7 years of burial: the concept of buried seed safe sites. Weed Science **58**:209-215.

Cook, G. D., S. A. Setterfield, and J. P. Maddison. 1996. Shrub invasion of a tropical wetland: implications for weed management. Ecological Applications **6**:531-537.

Cousens, R. and M. Mortimer. 1995. Dynamics of Weed Populations. Cambridge University Press, Cambridge, U.K.

Crawley, M. J. 1997a. Life history and environment. Page 83 *in* M. J. Crawley, editor. Plant Ecology. Blackwell Science Ltd., Malden, Massachusetts, USA.

Crawley, M. J. 1997b. The structure of plant communities. Pages 475-531 *in* M. J. Crawley, editor. Plant Ecology. Blackwell Publishing Ltd.

Crist, T. O. and C. F. Friese. 1993. The impact of fungi on soil seeds: implications for plants and granivores in a semiarid shrub-steppe. Ecology **74**:2231-2239.

Crowley, R. H. and G. A. Buchanan. 1982. Variations in seed production and the response to pests of morningglory (*Ipomoea*) species and smallflower morningglory (*Jacquemontia tamnifolia*). Weed Science **30**:187-190.

Csontos, P. 2007. Seed banks: ecological definitions and sampling considerations. Community Ecology **8**:75-85.

Csontos, P. and J. Tamas. 2003. Comparisons of soil seed bank classification systems. Seed Science Research **13**:101-111.

Dalling, J. W. and T. A. Brown. 2009. Long-term persistence of pioneer species in tropical rain forest soil seed banks. The American Naturalist **173**:531-535.

Dalling, J. W., A. S. Davis, B. J. Schutte, and A. E. Arnold. 2011. Seed survival in soil: interacting effects of predation, dormancy and the soil microbial community. Journal of Ecology **99**:89-95.

Dalling, J. W., S. P. Hubbell, and K. Silvera. 1998a. Seed dispersal, seedling establishment and gap partitioning among tropical pioneer trees. Journal of Ecology **86**:674-689.

Dalling, J. W., M. D. Swaine, and N. C. Garwood. 1998b. Dispersal patterns and seed bank dynamics of pioneer trees in moist tropical forest. Ecology **79**:564-578.

Darlington, H. T. 1922. Dr. W. J. Beal's seed-viability experiment. American Journal of Botany **9**:266-269.

Darlington, H. T. 1931. The 50-year period for Dr. Beal's seed viability experiment. American Journal of Botany **18**:262-265.

Darlington, H. T. 1941. The sixty-year period for Dr. Beal's seed viability experiment. American Journal of Botany **28**:271-273.

Darlington, H. T. 1951. The seventy-year period for Dr. Beal's seed viability experiment. American Journal of Botany **38**:379-381.

Darlington, H. T. and G. P. Steinbauer. 1961. The eighty-year period for Dr. Beal's seed viability experiment. American Journal of Botany **48**:321-325.

Darwin, C. 1859. The Origin of Species. The Genetics Society, London: Murray.

Davis, A., K. Renner, C. Sprague, L. Dyer, and D. Mutch. 2005a. Integrated weed management:"one year's seeding ... ." Extention Bulletin E-2931. East Lansing, Michigan: Michigan State University.

Davis, A. S. 2006. When does it make sense to target the weed seed bank? Weed Science **54**:558-565.

Davis, A. S. 2007. Nitrogen fertilizer and crop residue effects on seed mortality and germination of eight annual weed species. Weed Science **55**:123-128.

Davis, A. S. 2008. Weed seed pools concurrent with corn and soybean harvest in Illinois. Weed Science **56**:503-508.

Davis, A. S., K. I. Anderson, S. G. Hallett, and K. A. Renner. 2006. Weed seed mortality in soils with contrasting agricultural management histories. Weed Science **54**:291-297.

Davis, A. S. and S. Raghu. 2010. Weighing abiotic and biotic influences on weed seed predation. Weed Research **50**:402-412.

Davis, A. S. and K. A. Renner. 2007. Influence of seed depth and pathogens on fatal germination of velvetleaf (*Abutilon theophrasti*) and giant foxtail (*Setaria faberi*). Weed Science **55**:30-35.

Davis, A. S., K. A. Renner, and K. L. Gross. 2005b. Weed seedbank and community shifts in a long-term cropping systems experiment. Weed Science **53**:296-306.

Davis, A. S., B. J. Schutte, J. Iannuzzi, and K. A. Renner. 2008. Chemical and physical defense of weed seeds in relation to soil seedbank persistence. Weed Science **56**:676-684.

De Cauwer, B., T. D'Hose, M. Cougnon, B. Leroy, R. Bulcke, and D. Reheul. 2010. Impact of the quality of organic amendments on size and composition of the weed seed bank. Weed Research **51**:250-260.

Dekker, J. 1997. Weed diversity and weed management. Weed Science **45**:357-363.

Dekker, J. 2003. The foxtail (*Setaria*) species-group. Weed Science **51**:641-656.

Dekker, J., B. Dekker, H. Hilhorst, and C. Karssen. 1996. Weedy adaptation in *Setaria* spp. IV. Changes in the germinative capacity of *S. faberii* (Poaceae) embryos with development from anthesis to after abscission. American Journal of Botany **83**:979-991.

Donelan, M. and K. Thompson. 1980. Distribution of buried viable seeds along a successional series. Biological Conservation **17**:297-311.

Dyer, W. E., P. W. Chee, and P. K. Fay. 1993. Rapid germination of sulfonylurea-resistant *Kochia scoparia* L. accessions is associated with elevated seed levels of branched chain amino acids. Weed Science **41**:18-22.

Evans, J. A., A. S. Davis, S. Raghu, A. Ragavendran, D. A. Landis, and D. W. Schemske. 2012. The importance of space, time, and stochasticity to the demography and management of *Alliaria petiolata*. Ecological Applications **22**:1497-1511.

Everitt, J., M. Alaniz, and J. Lee. 1983. Seed germination characteristics of *Kochia scoparia*. Journal of Range Management **36**:646-648.

Facelli, J. M., P. Chesson, and N. Barnes. 2005. Differences in seed biology of annual plants in arid lands: a key ingredient of the storage effect. Ecology **86**:2998-3006.

Fenner, M. 1991. The effects of the parent environment on seed germinability. Seed Science Research **1**:75-84.

Fenner, M. and K. Thompson. 2005. The Ecology of Seeds. Cambridge University Press, Cambridge.

Foley, M. E. 2001. Seed dormancy: an update on terminology, physiological genetics, and quantitative trait loci regulating germinability. Weed Science **49**:305-317.

Forcella, F., B. R. Durgan, and D. D. Buhler. 1996. Management of weed seedbanks. Pages 21-26 *in* P. Kudsk, editor. Second International Weed Control Congress Copenhagen.

Forcella, F., K. Eradat-Oskoui, and S. W. Wagner. 1993. Application of weed seedbank ecology to low-input crop management. Ecological Applications **3**:74-83.

Forcella, F., R. G. Wilson, K. A. Renner, J. Dekker, R. G. Harvey, D. A. Alm, D. D. Buhler, and J. Cardina. 1992. Weed seedbanks of the U.S. corn belt: magnitude, variation, emergence, and application. Weed Science **40**:636-644.

Froud-Williams, R. J., R. J. Chancellor, and D. S. H. Drennan. 1983. Influence of cultivation regime upon buried weed seeds in arable cropping systems. Journal of Applied Ecology **20**:199-208.

Fu, X. 2002. Ecological evaluation of the restoration potential of slash-and-burn fallow fields in Xishuangbanna, SW China. Graduate University of Chinese Academy of Sciences, Kunming, Yunnan, China.

Fuerst, E. P., J. V. Anderson, A. C. Kennedy, and R. S. Gallagher. 2011. Induction of polyphenol oxidase activity in dormant wild oat (*Avena fatua*) seeds and caryopses: a defense response to seed decay fungi. Weed Science **59**:137-144.

Gallandt, E. R., E. P. Fuerst, and A. C. Kennedy. 2004. Effect of tillage, fungicide seed treatment, and soil fumigation on seed bank dynamics of wild oat (*Avena fatua*). Weed Science **52**:597-604.

Gallandt, E. R., M. Liebman, and D. R. Huggins. 1999. Improving soil quality: implications for weed management. Journal of Crop Production **2**:95–121.

Garcia-Orth, X. and M. Martinez-Ramos. 2008. Seed dynamics of early and late successional tree species in tropical abandoned pastures: seed burial as a way of evading predation. Restoration Ecology **16**:435-443.

Gardarin, A., C. Dürr, M. R. Mannino, H. Busset, and N. Colbach. 2010. Seed mortality in the soil is related to seed coat thickness. Seed Science Research **20**:243-256.

Ghersa, C. M. and M. A. Martinez-Ghersa. 2000. Ecological correlates of weed seed size and persistence in the soil under different tilling systems: implications for weed management. Field Crops Research **67**:141-148.

Goggin, D. E. and K. J. Steadman. 2012. Blue and green are frequently seen: responses of seeds to short- and mid-wavelength light. Seed Science Research **22**:27-35.

Gomes, L. F., J. M. Chandler, and C. E. Vaughan. 1978. Aspects of germination, emergence, and seed production of three *Ipomoea* taxa. Weed Science **26**:245-248.

Grant, C. D., D. T. Bell, J. M. Koch, and W. A. Loneragan. 1996. Implications of seedling emergence to site restoration following bauxite mining in western Australia. Restoration Ecology **4**:146-154.

Grenz, J. H., A. M. Manschadi, P. DeVoil, H. Meinke, and J. Sauerborn. 2005. Assessing strategies for *Orobanche* sp. control using a combined seedbank and competition model. Agronomy Journal **97**:1551-1559.

Grime, J. P. 1974. Vegetation classification by reference to strategies. Nature **250**:26-31.

Grime, J. P. 1977. Evidence for the existence of three primary strategies in plants and its relevance to ecological and evolutionary theory. The American Naturalist **111**:1169-1194.

Grime, J. P. 1981. The role of seed dormancy in vegetation dynamics. Annals of Applied Biology **98**:555-558.

Gross, K. L. 1990. A comparison of methods for estimating seed numbers in the soil. Journal of Ecology **78**:1079-1093.

Gross, K. L. and K. A. Renner. 1989. A new method for estimating seed numbers in the soil. Weed Science **37**:836-839.

Gruber, S., A. Buhler, J. Mohring, and W. Claupein. 2010. Sleepers in the soil-vertical distribution by tillage and long-term survival of oilseed rape seeds compared with plastic pellets. European Journal of Agronomy **33**:81-88.

Harper, J. L. 1977. Population Biology of Plants. Academic Press, London.

Harrison, S. K. and E. E. Regnier. 2003. Postdispersal predation of giant ragweed (*Ambrosia trifida*) seed in no-tillage corn. Weed Science **51**:955-964.

Harrison, S. K., E. E. Regnier, J. T. Schmoll, and J. M. Harrison. 2007. Seed size and burial effects on giant ragweed (*Ambrosia trifida*) emergence and seed demise. Weed Science **55**:16-22.

Hester, A. J., C. H. Gimingham, and J. Miles. 1991. Succession from Heather Moorland to Birch Woodland. III. Seed availability, germination and early growth. Journal of Ecology **79**:329-344.

Holloway, J. C., Jr. and D. R. Shaw. 1995. Influence of soil-applied herbicides on ivyleaf morningglory (*Ipomoea hederacea*) growth and development in soybean (*Glycine max*). Weed Science **43**:655-659.

Holm, L. G., D. L. Plucknett, J. V. Pancho, and J. P. Herberger. 1977. The World's Worst Weeds: Distribution and Biology. University of Hawaii, Honolulu.

Honda, Y. 2008. Ecological correlations between the persistence of the soil seed bank and several plant traits, including seed dormancy. Plant Ecology **196**:301-309.

Hughes, G. and J. L. G. Andujar. 1997. Simple rules with complex outcomes. Nature **387**:241-242.

Hulme, P. E. 1998. Post-dispersal seed predation and seed bank persistence. Seed Science Research **8**:513-519.

Karssen, C. M. 1982. Seasonal patterns of dormancy in weed seeds. Pages 243-270 *in* A. A. Khan, editor. The Physiology and Biochemistry of Seed Development, Dormancy and Germination. Elsevier, Amsterdam.

Kinter, C. L., B. A. Mealor, N. L. Shaw, and A. L. Hild. 2007. Postfire invasion potential of rush skeletonweed (*Chondrilla juncea*). Rangeland Ecology & Management **60**:386-394.

Kivilaan, A. and R. S. Bandurski. 1973. The ninety-year period for Dr. Beal's seed viability experiment. American Journal of Botany **60**:140-145.

Kivilaan, A. and R. S. Bandurski. 1981. The one hundred-year period for Dr. Beal's seed viability experiment. American Journal of Botany **68**:1290-1292.

Koornneef, M., L. Bentsink, and H. Hilhorst. 2002. Seed dormancy and germination. Current Opinion in Plant Biology **5**:33-36.

Kremer, R. J. 1993. Management of weed seed banks with microorganisms. Ecological Applications **3**:42-52.

Leck, M. A. and W. Schutz. 2005. Regeneration of Cyperaceae, with particular reference to seed ecology and seed banks. Perspectives in Plant Ecology Evolution and Systematics **7**:95-133.

Leishman, M. R., G. J. Masters, I. P. Clarke, and V. K. Brown. 2000. Seed bank dynamics: the role of fungal pathogens and climate change. Functional Ecology **14**:293-299.

Leon, C. S. 1980. A technique for estimating weed seed populations in cultivated soil. Weed Science **28**:134-138.

Leon, R. G. and M. D. K. Owen. 2006. Tillage systems and seed dormancy effects on common waterhemp (*Amaranthus tuberculatus*) seedling emergence. Weed Science **54**:1037-1044.

Lerner, P. and R. Peinetti. 1996. Importance of predation and germination on losses from the seed bank of calden (*Prosopis caldenia*). Journal of Range Management **49**:147-150.

Lewis, J. 1973. Longevity of crop and weed seeds: survival after 20 years in soil. Weed Research **13**:179-191.

Li, X., W. Liu, and C. Tang. 2010. The role of the soil seed and seedling bank in the regeneration of diverse plant communities in the subtropical Ailao Mountains, Southwest China. Ecological Research **25**:1171-1182.

Liebman, M., C. L. Mohler, and C. P. Staver. 2001. Ecological management of agricultural weeds. Cambridge University Press, Cambridge, UK.

Liew, T. H. 1973. Occurrence of seeds in virgin forest top soil with particular reference to secondary species in Sabah. Malaysian Forester **36**:185–193.

Lonsdale, W. M. 1993. Losses from the seed bank of *Mimosa pigra*: soil micro-organisms vs. temperature fluctuations. Journal of Applied Ecology **30**:654-660.

Lueschen, W. E. and R. N. Andersen. 1980. Longevity of velvetleaf (*Abutilon theophrasti*) seeds in soil under agricultural practices. Weed Science **28**:341-346.

Lueschen, W. E., R. N. Andersen, T. R. Hoverstad, and B. K. Kanne. 1993. Seventeen years of cropping systems and tillage affect velvetleaf (*Abutilon theophrasti*) seed longevity. Weed Science **41**:82-86.

Lutman, P. J. W., G. W. Cussans, K. J. Wright, B. J. Wilson, G. M. Wright, and H. M. Lawson. 2002. The persistence of seeds of 16 weed species over six years in two arable fields. Weed Research **42**:231-241.

Malone, C. R. 1967. A rapid method for enumeration of viable seeds in soil. Weeds **15**:381-382.

Mathias, A. and P. Chesson. 2013. Coexistence and evolutionary dynamics mediated by seasonal environmental variation in annual plant communities. Theoretical Population Biology **84**:56-71.

Menalled, F. D., M. Liebman, and K. A. Renner. 2006. The ecology of weed seed predation in herbaceous crop systems. Pages 297–327 *in* H. P. Singh, D. R. Batish, and R. K. Kohli, editors. Handbook of Sustainable Weed Management. Haworth Press, Binghamton,New York,USA.

Mirsky, S. B., E. R. Gallandt, D. A. Mortensen, W. S. Curran, and D. L. Shumway. 2010. Reducing the germinable weed seedbank with soil disturbance and cover crops. Weed Research **50**:341-352.

Mohler, C. L. 2001. Weed life history: identifying vulnerabilities. Pages 40 - 98 *in* M. Liebman, C. L. Mohler, and C. P. Staver, editors. Ecological Management of Agricultural Weeds. Combridge University Press, Cambridge, UK.

Moles, A. T., D. W. Hodson, and C. J. Webb. 2000. Seed size and shape and persistence in the soil in the New Zealand flora. Oikos **89**:541-545.

Mollard, F. P. O. and P. Insausti. 2009. Soil moisture conditions affect the sensitivity of *Bromus catharticus* dormant seeds to light and the emergence pattern of seedlings. Seed Science Research **19**:81-89.

Moravcova, L., P. Pysek, J. Pergl, I. Perglova, and V. Jarosik. 2006. Seasonal pattern of germination and seed longevity in the invasive species *Heracleum mantegazzianum*. Preslia **78**:287-301.

Moser, B. R., G. Knothe, S. F. Vaughn, and T. A. Isbell. 2009. Production and evaluation of biodiesel from field pennycress (*Thlaspi arvense* L.) oil. Energy and Fuels **23**:4149-4155.

Mulugeta, D. and D. E. Stoltenberg. 1997. Weed and seedbank management with integrated methods as influenced by tillage. Weed Science **45**:706-715.

Murdoch, A. J. and R. H. Ellis. 2000. Dormancy, viability and longevity. Page 183 *in* M. Fenner, editor. Seeds:The Ecology of Regeneration in Plant Communities. CABI Publishing, New York, USA.

Nathan, R. and H. C. Muller-Landau. 2000. Spatial patterns of seed dispersal, their determinants and consequences for recruitment. Tree **15**:278-285.

O'Tools, J. J. e. C., Paul B. 1983. Input to seed banks of proso millet (*Panicum miliaceum*) in Southern Ontario. Canadian Journal of Plant Science **63**:1023-1030.

Odum, S. 1965. Germination of ancient seeds: floristical observations and experiments with archaeologically dated soil samples. Dansk Botanisk Arkiv **24**:1-70.

Ooi, M. K. J. 2012. Seed bank persistence and climate change. Seed Science Research **22**:S53-S60.

Pakeman, R. J., J. L. Small, and L. Torvell. 2012. Edaphic factors influence the longevity of seeds in the soil. Plant Ecology **213**:57-65.

Peco, B., J. Traba, C. Levassor, A. M. Sánchez, and F. M. Azcárate. 2003. Seed size, shape and persistence in dry Mediterranean grass and scrublands. Seed Science Research **13**:87-95.

Pitty, A., D. W. Staniforth, and L. H. Tiffany. 1987. Fungi associated with caryopses of *Setaria* species from field-harvested seeds and from soil under two tillage systems. Weed Science **35**:319-323.

Pons, T. L. 2000. Seed responses to light. Page 237 *in* M. Fenner, editor. Seeds: the Ecology of Regeneration in Plant Communities. CABI Publishing, New York, USA.

Price, J. N., B. R. Wright, C. L. Gross, and W. R. D. B. Whalley. 2010. Comparison of seedling emergence and seed extraction techniques for estimating the composition of soil seed banks. Methods in Ecology and Evolution **1**:151-157.

Priestley, D. A. 1986. Seed Aging: Implications for Seed Storage and Persistence in the Soil. Cornell University Press, Ithaca.

Pringle, E. G., P. Álvarez-Loayza, and J. Terborgh. 2007. Seed characteristics and susceptibility to pathogen attack in tree seeds of the Peruvian Amazon. Plant Ecology **193**:211-222.

R Foundation for Statistical Computing. 2010. R: a language and environment for statistical computing. *In* R. D. C. Team, editor. http://www.R-project.org.

Radosevich, S., J. Holt, and C. M. Ghersa. 1997. Weed Ecology: Implications for Management. 2nd edition. John Wiley & Sons, New York, USA.

Rebek, K. A. and R. J. O'Neil. 2006. The effects of natural and manipulated density regimes on *Alliaria petiolata* survival, growth and reproduction. Weed Research **46**:345-352.

Rees, M. 1997. Seed dormancy. Pages 214-238 *in* M. J. Crawley, editor. Plant Ecology. Blackwell Publishing Ltd.

Roberts, H. A. 1981. Seed banks in soil. Advances in Applied Biology **6**:1-55.

Roberts, H. A. and P. A. Dawkins. 1967. Effect of cultivation on the numbers of viable weed seeds in soil. Weed Research **7**:290-301.

Sahid, I., Z. N. Faezab, and N. K. Ho. 1995. Weed populations and their buried seeds in rice fields of the Muda area, Kedah, Malaysia. Pertanika Journal of Tropical Agricultural Science **18**:21-28.

Schafer, D. E. and D. O. Chilcote. 1970. Factors influencing persistence and depletion in buried seed populations. II. The effects of soil temperature and moisture. Crop Science **10**:342-345.

Schafer, M. and P. M. Kotanen. 2003. The influence of soil moisture on losses of buried seeds to fungi. Acta Oecologica **24**:255-263.

Schutte, B. J., A. S. Davis, K. A. Renner, and J. Cardina. 2008a. Maternal and burial environment effects on seed mortality of velvetleaf (*Abutilon theophrasti*) and giant foxtail (*Setaria faberi*). Weed Science **56**:834-840.

Schutte, B. J., E. R. Haramoto, and A. S. Davis. 2010. Methods for optimizing seed mortality experiments. Weed Technology **24**:599-606.

Schutte, B. J., E. E. Regnier, and S. K. Harrison. 2008b. The association between seed size and seed longevity among maternal families in *Ambrosia trifida* L. populations. Seed Science Research **18**:201-211.

Schutte, B. J., E. E. Regnier, S. K. Harrison, J. T. Schmoll, K. Spokas, and F. Forcella. 2008c. A hydrothermal seedling emergence model for giant ragweed (*Ambrosia trifida*). Weed Science **56**:555-560.

Sears, A. L. W. and P. Chesson. 2007. New methods for quantifying the spatial storage effect: an illustration with desert annuals. Ecology **88**:2240-2247.

Sellers, B. A., R. J. Smeda, W. G. Johnson, J. A. Kendig, and M. R. Ellersieck. 2003. Comparative growth of six *Amaranthus* species in Missouri. Weed Science **51**:329-333.

Simpson, R. L., M. A. Leck, and V. T. Parker. 1989. Seed banks: general concepts and methodological issues. Pages 3-8 *in* M. A. Leck, V. T. Parker, and R. L. Simpson, editors. Ecology of Soil Seed Banks. Academic Press.

Sosnoskie, L. M. and J. Cardina. 2009. Laboratory methods for breaking dormancy in garlic mustard (*Alliaria petiolata*) seeds. Invasive Plant Science and Management **2**:185-190.

Spokas, K., F. Forcella, D. Archer, D. Peterson, and S. D. Miller. 2007. Improving weed germination models by incorporating seed microclimate and translocation by tillage. Proceedings of the Annual Meetingof Weed Science Society **44**:60.

Stallings, G. P., D. C. Thill, C. A. Mallory-Smith, and B. Shafii. 1995. Pollen-mediated gene flow of sulfonylurea-resistant kochia (*Kochia scoparia*). Weed Science **43**:95-102.

Sternberg, M., M. Gutman, A. Perevolotsky, and J. Kigel. 2003. Effects of grazing on soil seed bank dynamics: an approach with functional groups. Journal of Vegetation Science **14**:375-386.

Tang, Y., M. Cao, and X. Fu. 2006. Soil seedbank in a *Dipterocarp* rain forest in Xishuangbanna, Southwest China. Biotropica **38**:328-333.

Telewski, F. W. and J. A. D. Zeevaart. 2002. The 120-Yr period for Dr. Beal's seed viability experiment. American Journal of Botany **89**:1285-1288.

Thompson, C. R., D. C. Thill, and B. Shafii. 1994. Germination characteristics of sulfonylurea-resistant and -susceptible kochia (*Kochia scoparia*). Weed Science **42**:50-56.

Thompson, K. 1993. Persistence in soil. Pages 199-202 *in* G. A. F. Hendry and J. P. E. Grime, editors. Methods in Comparative Plant Ecology: A Laboratory Manual. Chapman & Hall, London.

Thompson, K. 2000. The functional ecology of soil seed banks. *In* M. Fenner, editor. Seeds: the Ecology of Regeneration in Plant Communities. CABI Publishing, New York, USA.

Thompson, K., J. P. Bakker, and R. M. Bekker. 1997. The Soil Seed Banks of North West Europe: Methodology, Density and Longevity. Cambridge University Press, Cambridge.

Thompson, K., J. P. Bakker, R. M. Bekker, and J. G. Hodgson. 1998. Ecological correlates of seed persistence in soil in the North-West European flora. Journal of Ecology **86**:163-169.

Thompson, K., R. M. Ceriani, J. P. Bakker, and R. M. Bekker. 2003. Are seed dormancy and persistence in soil related? Seed Science Research **13**:97-100.

Thompson, K. and J. P. Grime. 1979. Seasonal variation in the seed banks of herbaceous species in ten contrasting habitats. Journal of Ecology **67**:893-921.

Toole, E. H. and E. Brown. 1946. Final results of the Duvel buried seed experiment. Journal of Agricultural Research **72**:201-210.

Tsuyuzaki, S. and M. Goto. 2001. Persistence of seed bank under thick volcanic deposits twenty years after eruptions of Mount Usu, Hokkaido Island, Japan. American Journal of Botany **88**:1813-1817.

Tsuyuzaki, S. and F. Kanda. 1996. Revegetation patterns and seedbank structure on abandoned pastures in Northern Japan. American Journal of Botany **83**:1422-1428.

Ullrich, S. D., J. S. Buyer, M. A. Cavigelli, R. Seidel, and J. R. Teasdale. 2011. Weed seed persistence and microbial abundance in long-term organic and conventional cropping systems. Weed Science **59**:202-209.

Van Klinken, R. D., B. Lukitsch, and C. N. Cook. 2008. Interaction between seed dormancy-release mechanism, environment and seed bank strategy for a widely distributed perennial legume, *Parkinsonia aculeata* (Caesalpinaceae). Annals of Botany **102**:255-264.

Villiers, A. J. D., M. W. V. Rooyen, and G. K. Theron. 2002. Seed bank classification of the Strandveld Succulent Karoo, South Africa. Seed Science Research **12**:57-67.

Wade, M. R., G. M. Gurr, and S. D. Wratten. 2008. Ecological restoration of farmland: progress and prospects. Philosophical Transaction Royal Society B **363**:831-847.

Wagner, M. and N. Mitschunas. 2008. Fungal effects on seed bank persistence and potential applications in weed biocontrol: a review. Basic and Applied Ecology **9**:191-203.

Walck, J. L., J. M. Baskin, C. C. Baskin, and S. N. Hidayati. 2005. Defining transient and persistent seed banks in species with pronounced seasonal dormancy and germination patterns. Seed Science Research **15**:189-196.

Wiles, L. J., D. H. Barlin, E. E. Schweizer, H. R. Duke, and D. E. Whitt. 1996. A new soil sampler and elutriator for collecting and extracting weed seeds from soil. Weed Technology **10**:35-41.

Yao, S., H. Lan, and F. Zhang. 2010. Variation of seed heteromorphism in *Chenopodium album* and the effect of salinity stress on the descendants. Annals of Botany **105**:1015-1025.

Zorner, P. S., R. L. Zimdahl, and E. E. Schweizer. 1984. Effect of depth and duration of seed burial on Kochia (*Kochia scoparia*). Weed Science **32**:602-607.

APPENDIX

Table A1. Correlations between soil temperatures around the dormancy releasing period and the proportion of dormancy seeds (based on asin(x ^ 0.5) transformed dormancy data).

	Mean of soil temperatures				**Variance of soil temperature**			
	October to March		March to June		October to March		March to June	
	Slope	P value	Slope	P value	Slope	P value	Slope	P value
ABUTH	0.009	0.46	-0.005	0.70	-0.009	0.75	0.005	0.81
ALPET	0.039	0.83	0.217	0.16	-0.110	0.77	-0.287	0.22
AMATA	0.004	0.88	-0.002	0.94	0.025	0.66	0.011	0.78
AMBTR	0.108	0.18	0.108	0.20	-0.110	0.58	**-0.187**	**0.09.**
CHEAL	0.029	0.60	**0.078**	**0.08.**	-0.147	0.13	-0.097	0.17
IPOHE	-0.034	0.65	0.035	0.64	-0.097	0.53	0.028	0.80
KOCSC	0.200	0.36	0.007	0.98	-0.078	0.88	-0.176	0.62
PANMI	0.104	0.22	0.062	0.53	-0.035	0.87	-0.130	0.34
POLPY	0.119	0.31	0.154	0.17	**-0.392**	**0.04***	-0.188	0.28
SETFA	0.167	0.16	0.092	0.52	-0.086	0.78	-0.187	0.35
SETGL	0.105	0.32	0.027	0.82	-0.041	0.87	-0.116	0.49
THLAR	-0.058	0.53	0.064	0.50	-0.052	0.80	-0.042	0.77

Note: "*" significant at 0.05; "." significant at 0.10. ABUTH = *A. theophrasti*, ALPET = *A. petiolata*, AMATA = *A. tuberculatus*, AMBTR = *A. trifida*, CHEAL = *C. album*, IPOHE = *I. hederacea*, KOCSC = *K. scoparia*, PANMI = *P. miliaceae*, POLPY = *P. pensylvanicum*, SETFA = *S. faberi*, SETLU = *S. lutescens*, and THLAR = *T. arvense*.

Table A2. Correlations between soil matric potential (SMP) around the dormancy releasing periods and the proportion of dormancy seeds (based on asin(x ^ 0.5) transformed dormancy data).

	Mean of soil matric potential				**Variance of soil matric potential**			
	October to March		March to June		October to March		March to June	
	Slope	P value	Slope	P value	Slope	P value	Slope	P value
ABUTH	0.000	0.91	-0.000	0.69	0.000	0.65	0.000	0.59
ALPET	-0.005	0.60	0.003	0.45	0.001	0.53	0.002	0.59
AMATA	-0.002	0.17	0.000	0.89	0.000	0.15	-0.000	0.56
AMBTR	-0.006	0.20	-0.003	0.13	0.000	0.34	0.001	0.33
CHEAL	0.002	0.41	-0.001	0.54	0.000	0.40	0.001	0.39
IPOHE	0.003	0.40	0.001	0.69	0.000	0.27	-0.000	0.88
KOCSC	-0.012	0.30	-0.002	0.85	0.001	0.44	-0.000	0.93
PANMI	**-0.007**	**0.08.**	-0.003	0.17	0.001	0.21	0.001	0.40
POLPY	0.007	0.31	-0.003	0.28	-0.001	0.18	**0.003**	**0.09.**
SETFA	-0.010	0.13	-0.005	0.12	0.001	0.32	0.002	0.30
SETGL	-0.007	0.21	-0.001	0.66	0.000	0.33	0.000	0.95
THLAR	0.004	0.40	0.000	0.86	-0.000	0.60	-0.000	0.99

Note: "." significant at 0.10. ABUTH = *A. theophrasti*, ALPET = *A. petiolata*, AMATA = *A. tuberculatus*, AMBTR = *A. trifida*, CHEAL = *C. album*, IPOHE = *I. hederacea*, KOCSC = *K. scoparia*, PANMI = *P. miliaceae*, POLPY = *P. pensylvanicum*, SETFA = *S. faberi*, SETLU = *S. lutescens*, and THLAR = *T. arvense*.